VOLUME 135 PART 1 SEPTEMBER 1960

PROCEEDINGS

OF

THE ZOOLOGICAL SOCIETY OF LONDON

LONDON
PUBLISHED BY THE SOCIETY
SOLD AT ITS HOUSE IN REGENT'S PARK, LONDON, N.W. 1

Price Thirty Shillings

THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON

THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

Editor . . . . . L. HARRISON MATTHEWS, F.R.S.

Clerk of Publications . . . G. B. STRATTON, M.B.E.

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PHYLETIC WEIGHTING

BY

A. J. CAIN

Department of Zoology and Comparative Anatomy
University Museum, Oxford

AND

G. A. HARRISON

Anthropology Laboratory, Department of Anatomy
University of Liverpool

[Accepted 10th November, 1959]

The aim of the paper is to analyse the judgments involved in making phyletic classifications. It is shown that in addition to the phyletic information obtainable solely from comparative data, other evidence is often available which makes one conclusion about the evolutionary relationships of different forms more probable than others. This evidence principally bears on recognising and allowing for convergence and determining likely evolutionary changes. It comes from a knowledge of the geological age and geographical distribution of forms and from analyses of function, ecology, genetics and intra-superspecific variation. An understanding of the functional inter-relationships between structures and the ecological demands made on organisms is shown to be particularly important, since it makes possible the recognition of necessary correlations between characters, evolutionary trends, different adaptations to the same environment, and general improvements. A method is offered for quantifying the judgments where possible, and the procedure for constructing common ancestors is discussed.

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INTRODUCTION

One of the functions of the taxonomist is to produce classifications based on arrangements of forms which at worst are not inconsistent with evolutionary theory, and at best indicate the actual course of evolution within any given group. Unfortunately this actual course can be known with certainty only from a really adequate fossil record, which is seldom available. In many groups, it may be impossible to decide which of a multitude of arrangements that could be made is closest to the actual course of evolution, because that group is so badly known ; in such groups, only a " natural " classification, of the sort described by Cain & Harrison (1958) can be used. But when the fossil record is imperfect, it is felt that all the characters observable on the known forms cannot be given the same weight when one is trying to find the most probably phyletic arrangement, because it is known that some characters may fluctuate from form to form, while others remain stable. As Simpson (1945) remarks, characters are always " selected, weighted and interpreted ".

The purpose of this paper is to examine the ways in which phylogeny can be inferred, to make the methods of weighting quantitative where possible, and to derive a definite procedure that will make explicit the judgments of the taxonomist engaged in phyletic arrangement and classification. The various sorts of evidence bearing on the phylogeny of a group are of course well known, but the analysis of their various relevances and of the method of using them quantitatively is believed to be new.

DEFINITION OF TERMS

Several taxonomic terms have more than one meaning. To avoid confusion, it is sometimes necessary to distinguish these meanings and assign new terms to them. The following definitions will be found necessary in the course of this paper.

(a) *Arrangements and classifications*

The word classification is used at present both for the activity of classifying, and for the result, and often also for merely placing forms which are alike near each other in some way without actually delimiting discrete classes. The problems of defining classes are not dealt with in this paper. We distinguish the activity of placing forms near to or far from one another on their resemblances as arrangement, and this word can be used also for the result of doing so.

(b) *Phyletic and phenetic arrangements*

A classification or arrangement which is based on a few convenient characters for the purposes of sorting or identification has always been called an artificial classification, as opposed to a natural one, but the term " natural " in this context has had several different meanings. When an arrangement is based on all the observable characters of the forms concerned, i.e. on overall similarity, it has been called natural (e.g. by Gilmour 1940, 1952, Sneath 1957, and Cain & Harrison 1958). But in the last hundred years, a phylogenetic arrangement or grouping has usually been called natural (e.g. by Michener & Sokal 1957, p. 155). Before the coming of evolution, the word had other meanings (Cain 1958, 1959 a, b). Following a suggestion by Mr H. K. Pusey,

we shall refer to the arrangement by overall similarity, based on all available characters without any weighting (Cain & Harrison 1958) as *phenetic*, since it employs all observable characters (including of course genetic data when available), and that which aims to show the course of evolution as *phyletic*. When a good fossil record is available, of course, the whole evolutionary dendrite can be worked out for that group simply by putting those forms together that are most alike phenetically, without any phyletic weighting. For such groups, the phenetic and phyletic arrangements are the same, and the only problem for the taxonomist is how to classify, how to break up the dendrite into separate groups for the accepted categorisation into genera, families and so on, and for naming.

(c) *Cladistic and patristic affinity*

There are two components in phyletic affinity which need to be distinguished clearly. If two forms are said to be phyletically closely related, they may be very similar because they both possess many characters which they have inherited from a common ancestor, or they may have diverged from a common ancestor which itself was not the common ancestor of other forms in the group in which they occur, so that if one descends the phyletic line from one of them, the first junction is with the phyletic line from the other, not with a line from any third form. Consequently in terms of phyletic lines they are directly related, even though (in contrast to the other meaning just given), they may have diverged further apart than one of them has from other members of the group on different phyletic lines, which have diverged from it only a little. Similarity due to common ancestry, not to convergence, can be called patristic. Closeness of relationship in terms of phyletic lines can be called cladistic (cf. the definition of clades by Huxley, 1959). Patristic similarity, therefore, is one form of similarity, the other being convergent. 'Cladistic' refers to the paths by which a given similarity has been attained.

THE ACTIVITIES INVOLVED IN PHYLETIC ARRANGEMENT

As already mentioned, if the complete or nearly complete fossil record of a group is known, no weighting is needed to produce a phyletic arrangement of it. All that is necessary is to take any form and see which others on overall similarity are most like it, and place them next to it. Then their closest relatives can be found and placed next to them, and so on until the whole of the evolutionary dendrite has been revealed. This procedure could be upset only if two forms had converged so as to become identical, which is unlikely. No information other than the characters observable on the forms would be necessary to work out the dendrite, and only absolute dating of the forms would add anything of phyletic interest ; this would give us the actual rates of evolution of the lines.

Such a situation is in practice rare, but the fossil record of some groups is so nearly complete that little remains to be guessed. Far more often, however, there are many large and small gaps in the record as we have it, and then all relevant evidence must be used to make a phyletic arrangement. That is the situation dealt with in this paper.

Three separate activities can be distinguished in the production of a phyletic arrangement. Firstly, some of the characters used in making a

simple phenetic arrangement give us no phyletic information, and can be removed. What is left is the necessary evidence on which we have to detect as much convergence as we can. Resemblance due to convergence is precisely that not due to inheritance from a common ancestor. In general, phenetic resemblance can be separated into patristic and convergent resemblance, and the latter must be discarded when we are arranging our forms phyletically. The corrected arrangement will tell us what forms are like each other patristically, and what are not, even though their phenetic resemblance is great, because they are convergent. Lastly, when we have obtained our patristic arrangement, we may have various sorts of evidence by which to judge what phyletic lines should be drawn to connect the groups and fill in gaps. It is one thing to know that two forms are more close patristically to each other than to a third, but we may still need to know whether the third arose from the common ancestor of the first two, or by more rapid evolutionary change from one or other of them. All information bearing on rates of change, relative times of divergence, or characters excluding a particular form from being part of a given line, are important in working out cladistic affinity.

What can be done depends on what evidence is available and will not be the same from group to group. Some groups are so badly known that only a phenetic arrangement is possible. In others, some evidence of convergence and cladistic affinity may be available, in yet others we may be able to give a reasonable account of the course of evolution. The taxonomist who specializes in a difficult group may feel inclined to deny all possibilities of phyletic arrangement in any group. Some botanists seem to take almost this attitude, but a study of some vertebrate groups might show them that it is sometimes possible. In a few examples, as mentioned above, the record is complete enough for no weighting to be required, and for the phenetic arrangement to reveal the course of evolution.

When an evolutionary dendrite has been constructed, one can see what common ancestors are unknown, and try to supplement it by reconstructing them. This has often been done, sometimes very uncritically, in the past, and possible procedures are considered briefly in the present paper. Lastly, the taxonomist is faced with the problem of breaking up the dendrite into discrete classes, in order to give them the names which are the internationally accepted reference-symbols for plants and animals. The problems which this activity raises are not discussed here.

PHYLETIC INFORMATION OBTAINED FROM COMPARATIVE DATA

(i) *Convergence*

The basic data that one has for the phyletic study of a group are the actual specimens that attest that such a group has ever existed. A comparison of the similarities and differences of the forms recognized can itself, without any weighting of the evidence, give a great deal of evolutionary information in many groups, showing us good examples of convergence, divergence and parallelism. The resemblance of bats to other mammals, for example, and the fact that they show some convergence with birds in their organs of locomotion, was worked out purely on their comparative anatomy before the theory

of evolution was thought of. From the point of view of the phylogenist, the principal disadvantage of a phenetic arrangement based on imperfect material is that some examples of convergence may go unrecognized and the forms involved be put into a single group, which is then mistakenly thought to be monophyletic. On the other hand, in a phenetic classification divergence should be as well recognized as if the record were complete ; and of course, what convergence can be recognized is pure gain for the phylogenist. It is the unrecognized convergence or parallelism that causes trouble ; in what follows, where we refer to convergence, parallelism is included as a special case. In recent years, comparative morphology has been notably supplemented by other comparative studies, in serology, biochemistry, behaviour and genetics, for example. All these provide evidence which can be used in comparing various forms, and may or may not support the arrangement arrived at from comparative morphology alone. They can rarely give direct evidence of phyletic affinity, nor can any one of them be regarded as invariably more trustworthy than the rest, since none is known to be free from all possibility of convergence. Everything said of comparative morphological data in this paper applies equally to comparative data of any other sort.

We may agree to the general proposition that convergence producing extreme similarity is more likely between closely related than between distantly related forms, simply because the chances of distantly related, and therefore very different, forms being modified over a sufficient period of time always in the direction that will enable them to occupy precisely the same niche, are obviously less than for already closely related ones, which may very well come to occupy the same niche (in different areas). But we have no way of estimating these probabilities ; even if we had, we should obtain only probabilities ; it might be impossible to say just what had happened in any one instance, without a very complete knowledge of the ecologies of the forms concerned over a long time, which we are not likely to have. If convergence between closely related forms is likely to be relatively common, an arrangement by overall affinities of an imperfectly known group will often hide this fact. Forms which are very similar and certainly not distantly related will be grouped together automatically and regarded as alike entirely because of a common proximal ancestor, not because of convergence in part ; more phenetic resemblance will be regarded as patristic than is really so. Consequently the detection of convergence is probably the most important thing in correcting the present methods of arrangement for inherent bias, before attempting a phyletic arrangement. (Convergence is also of importance in evolutionary studies as bearing directly or indirectly on competition and extinction, but this is not relevant in the present paper).

But if it is true that convergence is more likely between closely related than between very dissimilar forms, it follows that in imperfectly known groups, we may often be unable to detect it. In general, it is likely that we shall underestimate it, and there may be no way whatever of checking this. It is usually taken that resemblance in a large number of characters not functionally related is a good indication of monophylety. An outstanding example is the amazing complex of morphological characters seen in the salivary gland

chromosomes of Diptera. The number and relative lengths of the chromosomes, the positions of their centromeres, and above all the vast number of bands of different intensity and spacings, give such a multitude of characters to be observed, that it is unbelievable that two specimens with the same characters are not very closely related. Similarly, where a special organ of great complexity has been evolved to deal with some particular function in a given form, and an organ almost identical in all its characters is found in a second, the two forms would not usually be thought to have converged. The judgment is being made here that if the organ is developed at all, there is no necessity for all its details to be the same in two forms unless they are closely related, and then the detailed resemblance can be taken as patristic. But of course however complex the organ, if it could be shown that all the details were necessary functionally and could not vary, then the resemblance might be either convergent or ancestral (patristic).

The actual detection of convergence by means of comparative data is fairly simple. The phenetic classification on overall affinities shows that some groups are, overall, very distant from each other, but nevertheless have a few characters in common. If these groups have almost nothing else in common, we say that these characters in these groups seem to be convergent. An example used by Darwin is the fish-like shape and " fins " of the whale as compared with those of teleost fishes. This conclusion is strengthened if we also know other groups which, having a strong affinity with one or other of the groups with convergent characters, are clearly their close relatives and serve to bridge the gap between them and the other group, but do not have those characters which are believed to be convergent. For example, if we did not know the reptiles and amphibia, it might be well worth considering whether the whales are not the most primitive of the mammals because of the characters in which they resemble fishes ; but the existence of the amphibia and therapsid reptiles makes this suggestion seem incorrect merely on their overall affinities.

(ii) *Primitive characters*

Darwin made the point explicitly in the ' Origin of Species ' that in a phenetic group, especially if the different forms live under very diverse conditions, those characters which are held in common cannot be adaptations to particular modes of life and are reasonably explained (although the inference is not, of course, completely certain) as inherited from a common ancestor, i.e. as primitive. It would follow from this that some idea of which characters are primitive in the group can be obtained by listing all the characters common to the group and disregarding all the inconstant ones. Darwin was apparently too cautious to make this step explicitly.

This method of attempting to determine which characters are primitive in a given group, and thereby the direction of evolution, has been widely used. But it makes no allowance for parallelism and convergence, and has been severely criticized (Bather 1927, Gilmour 1952, Bigelow 1956, 1958). It assumes in effect that if any change has taken place in the group concerned, it is always divergence ; and it is true that if there were no parallelism or convergence in a group, then the use of only overall affinity, even in an

imperfectly known group, would produce a more nearly phyletic arrangement of the forms. Darwin's ideas on this point are examined by Cain (1959 b).

Sometimes the anatomical topology of an organ or system in a number of forms suggests the probable condition of this organ or system in the common ancestor of these forms. For example, the single right aortic arch of birds and the single left aortic arch of mammals would point by themselves (all other characters agreeing that these groups had a common proximal ancestor) to an ancestral condition in which both aortic arches were present. It would be difficult to visualize a change-over from a single left to a single right arch with no other structures showing any sign that the arch had crossed the midline. This sort of evidence can often be obtained when an organ in two or more forms shows mutually contradictory qualifications of a more generalized state, which is then taken to be primitive.

Where a certain amount of fossil evidence is available, and on occasion when it is not but some primitive forms have persisted to the present day with little change, we may be able to construct some phenetic groups which show definite trends converging on each other. This is especially likely when we are dealing with a group undergoing strong adaptive radiation (although we do not know the functional interpretation of the radiation), in which there are various lines specializing in different directions and urged on by competition with each other, so that a sudden diversion of direction in any one line is unlikely, and convergence still more so. Recognition of this pattern of diverging lines, especially when there is a large number of them, suggests immediately (a) that we are dealing with a single monophyletic group showing adaptive radiation, and (b) that the characters in which those forms in different lines that are most alike resemble each other are the primitive characters in this group. Where there are only a few lines, one must be careful that one is not dealing with convergence and reading the lines the wrong way round. Dating (where possible) will correct the direction.

It is perhaps unfortunate that the excellent example of the fossil history of horses (see e.g. Simpson 1951 a) is so well known. This and other groups of mammals show this type of evolutionary pattern, although, as Simpson says, the actual course in the horses is by no means simple, and has been much misrepresented. But where much extinction has taken place in a group, extrapolation of trends applied to an imperfect record may lead us grossly astray. This method requires that the trends observed have been uniform in direction since their initial divergence, which may not be right, and requires enough evidence for these trends to be correctly recognized. The method of common characters, on the other hand, has to assume that phenetic groups are also monophyletic, which is far more likely to be incorrect ; but often it is the only method usable.

The reason for trying to identify primitive characters is that they are undoubtedly responsible for patristic resemblance, and that very close patristic resemblance between two forms may tend to conceal the fact that a third form which has lost many of its patristic characters may nevertheless be cladistically more closely allied to one of the two forms retaining them than to the other. Consequently, patristic similarity needs further scrutiny before

cladistic relationship can be determined. For example, *Australopithecus* may agree more closely with the great apes than with modern man, not by convergence, but because it still has a large number of primitive characters ; but other evidence leads us to suppose that the human line came from the australopithecine, and these two are therefore more close cladistically to each other than is either to the great apes' lines.

(iii) *Summary*

In short, a phenetic group, if there is no evidence to the contrary, can be taken as monophyletic by those who wish. It would seem unlikely that the very natural group of birds, for example, is polyphyletic, and superfluous to assume that the numerous characters common to all members of it have arisen on several occasions (even if they did). Those who dislike this procedure must simply label such groups as phenetic, not phyletic, and leave it at that. But when there is evidence from any data that a resemblance in certain characters is convergent, then any group based on them is known not to be monophyletic, however valid phenetically it may be. And when there is evidence, from anatomical topology or trends, that certain groups of characters within a phenetic group are primitive, the subgroup of forms that possess them is likely to be monophyletic. If we can construct a set of trends, some cladistic information can be obtained from it. But unless we have so many forms that phyletic lines can be constructed phenetically, no further information on cladistic relations can be obtained from purely comparative data.

CLASSES OF SUPPLEMENTARY INFORMATION

In an imperfectly known group, the inadequate comparative data can be supplemented by any other data which indicate either further possibilities of convergence or possible lines of descent. Such data can be obtained from various subsciences of biology and from other disciplines, and data from a single subscience, e.g. physiology, may be used for phyletic weighting in different ways. Four main classes of data are recognized here. After discussion of each, their relevance for the different activities involved in phyletic classification recognized above is summarized in a separate section.

(i) *Time*

How closely two forms resemble each other patristically depends only on the characters they possess, allowance having been made for convergence, not on their relative times of occurrence, since rates of evolution vary greatly and a given amount of divergence may be produced rapidly in one line and very slowly indeed in another. Actual dating is essential to tell us the different rates of evolution that have been working in the group. This in itself is of great evolutionary interest but need not give us useful information about the derivations of the forms in the group.

The principal use of time in phyletic classification is to give the direction of evolution, to show which form in a morphological series which could be read in either direction (or indeed from the middle outwards in both directions) is the first in time and most likely to be ancestral. This may bring to light

examples of probable convergence, and therefore some further cladistic information. One example is the relation between *Homo sapiens* and *H. neanderthalensis*. Let it be granted that there exists a sufficient number of intermediates between classical Neanderthalers and progressive Neanderthalers to make certain the origin of one from the other, but that merely on this evidence we do not know which gave rise to which. Then on the purely morphological evidence the simplest arrangement of these and related forms is :—

H. sapiens
progressive Neanderthalers
classical Neanderthalers
Pithecanthropus

But on the known time relations, using relative or absolute dating, the arrangement must be

classical Neanderthalers *H. sapiens*
progressive Neanderthalers
Pithecanthropus

in which case the resemblances between classical Neanderthalers and *Pithecanthropus* must be convergent. The time relations must be obtained from data entirely independent of the comparative morphological data observable on the specimens. Any attempt to use the comparative data as a substitute for time must presuppose a certain arrangement, and cannot then be used to discover it.

Time as such may be of surprisingly little value in tracing a given phylogeny. There is one obvious axiom which can always be applied, namely that no form can appear in the fossil record before it has evolved. Consequently its discovery in strata earlier than those from which it was previously known may necessitate a considerable redrawing of the accepted phyletic diagram. An example would be the discovery of Triassic lizards. But its discovery in much later strata or alive at the present day (e.g. the coelacanth *Latimeria*) means very little since it is well known from living material that comparatively primitive forms may persist long after their close relatives have become extinct or transformed to different descendants. It is true that no more conclusive evidence of the disappearance of a form could be obtained than the demonstration that it had transformed into a different one, but it is exceedingly difficult to be sure that this has been observed for the world population of the form concerned. Absence from the fossil record, as in the coelacanths now living, may mean nothing at all, and the fact that in some strata a given form can be seen to transform into another does not mean that it cannot have persisted unchanged elsewhere. Oakley (1954) comments on the known australopithecine remains that the earliest known are not old enough to have been ancestors of the first tool-making hominids, but he cautiously and rightly adds " It is quite possible that older species of the genus were ancestral to a more progressive line which evolved into larger-brained, tool-making types (" men " in common parlance) ; but if so they remain to be discovered—and not necessarily in *South* Africa ". This is the converse of the situation discussed above ; the occurrence of two forms as near contemporaries does not mean that one of them cannot be a persistent population of a form which also gave rise to the other.

The most usual evidence of time is given by stratigraphy, but absolute dating is now making great strides (see e.g. Zeuner 1958). Some other methods of relative dating may be mentioned. Where it can be seen that two or (rarely) more species have arisen in an isolated area as a result of multiple invasion by the same stock (Mayr 1942) it is usually taken that the most modified of these isolated forms is the oldest. This gives a relative dating for the forms. Also, where it can be seen that of two overlapping inversions in a chromosome one must have arisen later than the other because it involves the other, we have an actual sequence in time. Again, when a zone of secondary hybridization can be recognized, it is clear evidence that the forms concerned have diverged in isolation and come together secondarily, the hybrid forms being produced later than the parents. But these examples require for their recognition evidence which is to be found only, or almost only, in living forms, and cannot help except under this restriction.

When barriers can be dated (e.g. ice-sheets, deserts, mountain ranges, or ingressions by the sea) and two forms can be seen to be geographical representatives on either side of the barrier, their production may be reasonably ascribable to speciation on either side of the barrier, and this may allow some relative dating. Occasionally, some evidence bearing on convergence can be obtained from a combination of time and geographical distribution, when a dateable barrier separates forms which are known to have been produced subsequently to it and are very similar. These must then be convergent in their similarity (unless after all the barrier was once passable by them). An example is given by the monkey-like lemur *Archaeolemur* of Madagascar. The appearance of true Old-World monkeys on the mainland of Africa seems to be later than the separation of Madagascar from Africa by the sea. It is likely therefore, that this similarity between forms on the mainland and in Madagascar is due to convergence. Such combinations of time and geological evidence may be very valuable.

(ii) *Distribution*

When a form is found geographically far away from all other members of its group, it is always worth considering whether we are dealing with a case of convergence, especially when there is evidence of a strong barrier to the dispersal of the group. Marsupial moles bear a strong resemblance to the talpid moles of the Palaearctic. Nevertheless, they are directly related not to them but to other mammals in their own region of occurrence. Earlier ornithologists described many Australian birds as thrushes, wrens, etc., because of a resemblance to western Palaearctic birds ; and various remarkable relationships were ascribed to the Mexican carnivore *Bassaris* ; but these are now regarded after more study as products, so to speak, of local stocks.

But such a situation is best regarded only as giving warning of the need to check the affinities of the forms concerned, since of course there are many groups which do show highly disjunct distributions as a result of fragmentation of range. The zalambdodont insectivores, formerly represented also in Asia and North America, are now confined to Africa, Madagascar, and the West Indies ; and the marsupials, once in Europe, are now in Australasia and

America (mainly South America). Even the characteristically South American notoungulates had two representatives in Asia and North America, which suggests that one form at least was able to surmount the barriers isolating South America. A slight change in ecological tolerance may allow one member of an otherwise imprisoned group to get out. Earthworms in general are killed by salt water, but a few unrelated forms have become tolerant to it, and some are now circummundane in the warmer parts of the world (Stephenson, 1930).

In general, geographical distribution may serve to call our attention to cases requiring investigation, but they must be decided on the comparative data. However improbable a distribution may seem, we know too little about the detailed history of the earth's surface and the powers of dispersal of particular forms over a long time to be able to rule it out. If there is no doubt on the morphological evidence that alligators are now confined to China and *Eastern* North America, or the peacocks to the Orient and the Congo forests, we must just accept the distributional facts meekly. Apparent anomalies of distribution can inspire us to get further evidence from other data, but can hardly cause any weighting of these data.

(iii) *Necessary correlates*

When it can be seen that several distinct characters (in the sense explained by Cain & Harrison, 1958) are varying together because they are necessarily correlated, we can recognize that variation in any one must be accompanied by corresponding variation in all the others. Then we can put no weight on them as separate characters, because if one arises by convergence in a different and unrelated form, but fulfilling the same function, all the others will arise as well. They cannot be taken as a large number of unrelated characters, most unlikely to have been all attained by convergence.

For example, in many mammals there is a necessary functional correlation between the shape of the posterior face of the lower canine and the anterior face of the upper, which act together as a shearing device. In fact wherever teeth come together for shearing or chopping by a simple movement of apposition, there must be a correspondence between the opposing or shearing surfaces, sufficient for the animal to persist in a given biota. If the shape of the opposable surfaces of one tooth is specified, that of its opposite is in effect determined also, and no doubt given the mechanical properties of enamel and dentine, some part at least of the body of the tooth, which has to be mechanically sound, is also specified although it might be very difficult to forecast the exact characters of one tooth from a specification of the other. Consequently, one would not use many of the characters of such teeth as independent evidence for determining possibilities of convergence, and it would be wise to neglect not only the shape of the opposing surfaces but also other characters of the body of the tooth as under suspicion. Even if the shearing or chopping could be carried out equally efficiently for the purposes of survival by several minor variants, so that some free variation were permissible, it might be advisable to disregard all the characters of one of the opposing teeth as probably largely functionally correlated, even though this could not be proved. Where, however, there is no necessary correlation, as

in the use by one form of the fourth upper premolar and first lower molar as carnassial teeth (as in modern carnivores) but of different teeth for the same function in other forms (e.g. first upper molar and second lower molar in some creodonts) the variation is not to be disregarded in examining for convergence. But since the exigencies of flight require that the wings of birds should be symmetrical, one does not reckon similarity in some character of the left-hand wing and then separately of the same character in the right-hand wing.

Of course, if the function changes, the correlation between characters may disappear completely or be replaced by a different one. Two canines, for example, may cease to bite against one another and turn outwards as tusks, whose shapes may be completely independent functionally.

It is quite possible that many such functionally necessary correlates escape us at present because either we do not see the functional significance of particular characters, or we do not see that they are necessarily correlated. Mr H. K. Pusey points out to us that most of the major features characteristic of mammals, though not their details, may well be necessarily correlated as a consequence of high activity, which requires homoiothermy. To maintain a high body temperature will require a high minimum rate of intake of food, and (unless the body temperature is temporarily lowered, as in those mammals that hibernate) periods of starvation will be far less readily tolerated than in cold-blooded animals living on the same food. Consequently we see the production of molars, to render the food more rapidly digestible, and the production of a hard palate so that the animal can chew while breathing (since the rate of supply of oxygen must also be high). The heterodonty requires a more versatile jaw-suspension allowing a shift of the applied muscular forces to different parts of the jaw according to which sorts of teeth are being used at a time, which means abandoning the old reptilian hinge—and this allows the development of ear ossicles from the freed bones, but one cannot say that this was a necessary consequence. A more mobile jaw-suspension requires larger muscles to hold the jaw firmly in its various positions ; larger muscles may well also be necessary for the efficient functioning of blunt molars and premolars, which require more force to work them against each other than do sharply pointed teeth to bite into food, and may be in action for long periods. The larger muscles mean an enlargement of the temporal fossae, with reduction of the outer dermal bones to a zygomatic arch, and in consequence there must be an extension of bones to complete the cranium laterally both as a protection for the brain and as an area of insertion for part of the enlarged muscles. Granted a therapsid condition to begin with, all these changes may well be necessary functional consequences of homoiothermy, and therefore may well have all evolved together more than once in this stock.

This does not mean that homoiothermy can arise only if the mammalian modifications can be evolved ; in fact it occurs in birds in association with very different modifications. But it does mean that, given an ancestral condition, if numerous characters must evolve together as functional correlates, then they may well have done so from the same ancestral stock several times over. The actual correlation need not, of course, be that required to give perfectly efficient functioning, but only to allow the possessors to survive in

competition with their contemporaries, which may themselves be imperfect. Early terrestrial "swift-moving" carnivores may have moved at only five miles an hour if their prey moved at only four.

As we have pointed out before (Cain & Harrison 1958), if two or more characters are observed to be correlated in a group, this does not always mean that they are necessarily correlated. Grazers on open plains may all require a mechanism for rapid locomotion to escape their predators, and the same mechanism may be found throughout a monophyletic group. But this does not mean that the possession of grazing teeth automatically produces the *equid* foot, for example ; the artiodactyl foot is also very often found in such situations. Similarly, to be an arboreal leaf-eater may necessitate both pouches for storing food and some prehensile apparatus ; but either cheek-pouches or a sacculated stomach may be used for the one, and prehensile hands and feet (with or without a prehensile tail) or large hooked claws could be used for the other. The correlation of different apparatus for performing different functions may be necessary since the animals concerned could not persist without it, but the modes of carrying out each function may still be free, and can be used in testing for phyletic affinity. For example, all birds must have some mode of feeding, somewhere to put their eggs during incubation, some form of intercommunication for courtship, etc. But if we find a number of birds all sucking nectar from flowers, all with cup-nests of very similar construction, all with the same sort of song, and all with similar plumage-patterns, then since the particular mode of feeding, style and details of nest, etc., can reasonably be regarded as independent of each other, we would regard the phenetic group of such birds as probably monophyletic, having regard to their similarity in so many independent details.

If there is an environment so stringent that it dictates not only what functions must be employed but also every detail of them, then the ecological correlation of the resulting characters could no more be used as evidence for or against convergence than could a necessary correlation within a single function. Clearly, the most detailed knowledge of function and ecology is desirable when we are testing for convergence (Cain, 1959 c).

If our knowledge is sufficient, we may be able to see that a particular function is not wholly specified in a given environment but can be carried out in only a very few alternative ways. (We must be sure, however, that these ways are completely equivalent, and not different specializations for slightly different environments, and this may be almost impossible to establish.) If only a very few ways are possible, it might be felt that convergence is far more likely than if the function can be carried out in many different ways, since in the latter case two forms carrying it out in the same way are more likely to do so because of patristic resemblance, whereas if there were only two possible ways (say) convergence might well occur. It is doubtful, however, whether one can usually determine with certainty all the possible ways, theoretically, of doing any one thing.

(iv) *Information on likelihood of change*

This is a large class of rather miscellaneous but very important evidence bearing on whether a given form is likely to be able to give rise to another, and if so, whether quickly or only slowly.

(a) *Function and ecology*

If unrelated forms occupy the same niche, it is very likely that they will come to possess similar characters in respect of the functions necessitated by that niche. Both porpoises and large teleosts chase and catch fish in the sea, and will therefore resemble each other to some extent. But those characters which are comparatively independent of the demands made by one particular environment are not likely to be affected, and, as Darwin said, these will be of special value in determining phyletic relationships, since they are likely to be patristic. Differences in them may well point to a longstanding separation of stocks.

For example, the chrysochlorid and talpid moles resemble each other both in being moles and in being insectivora. From a functional analysis we can identify the characters required by a mole-like mode of life, and can see that they may well be convergent in these forms. The general insectivore characters in which they agree, however, have not been shown to be particular adaptations and are likely, therefore to show patristic resemblance ; in these characters, they differ greatly from the marsupial mole. (In fact in this example, the patristic characters do indicate that within the Insectivora, the chrysochlorids and talpids belong to different stocks, which tends to confirm that their mole-like characters are convergent.)

Conversely, if the differences between two forms can be seen on functional analysis to be due to a difference of particular environments, as for example the otter is clearly close to the weasel and stoat but modified for an aquatic environment, these differences, if all other characters are similar in the forms compared, can be regarded as subsequent modifications imposed upon an ancestral type. It may also be thought that they may have been acquired quite rapidly, and need not point to a phyletic separation of long standing.

If in a given group, a trend towards greater efficiency in some particular function can be seen, and there is a related group of much more primitive forms, all very alike but one of them showing some specialization for this same function, then this form may well be regarded as the beginner of this trend and assigned phyletically to the series showing it, although in all its other characters it is more similar to the other unspecialized forms. This employment of functional trends for completing phyletic lines has been emphasized by Le Gros Clark (1955). As he points out, the result may be only an approximation to the truth, since the fossil forms actually available may be not on the phyletic line but on sidebranches from it, and a line drawn through them will run more or less parallel to the actual line but will not be it. Perhaps the best example of this is the recognition by T. H. Huxley in 1872 and Kowalevsky in 1873 of the line *Palaeotherium–Anchitherium–Hipparion–Equus* as the phyletic line of the modern horses. But the working-out of the American fossil record showed that the first three were sidebranches, and the line lies through *Orohippus*, *Miohippus*, *Merychippus*, and *Pliohippus* to *Equus* (see e.g. Simpson 1951 a).

The implied basis for this use of function is that specialization has occurred to such an extent in a given line in a given biota that further progress is likely for that stock only in the same direction. The expression " highly specialized "

is used in two ways, to refer either to a remarkable peculiarity of structure irrespective of function or in addition to it) or to specialization for a particular function. The first should rather be called a " singularity ". For example, the mammalian ear ossicles are remarkably constant in their various characters through the group of mammals, and are a peculiarity not paralleled in any other vertebrates (except remotely in the carp). The judgment that they could hardly have arisen independently in other forms, and therefore that anything having them must be a mammal, is simply that here we have a highly complex system which is unlikely to have arisen more than once. This judgment belongs to the class of weightings based on comparative data. But the observation that the horse has its digits reduced to one on each limb, and that that one is hoofed, suggests, when we survey the functions carried out by other tetrapod limbs, that the horse is greatly restricted in its evolutionary possibilities. Such a foot is excellent for running and kicking, but not for grasping or flying, and is of little use for swimming, digging or climbing well (although we may find it necessary to be cautious in what we say about the last three functions). Such a specialization of function suggests that the horse, as compared with the opossum of North America, for example, is more liable to extinction with a change in environmental conditions, and less able to give rise to an adaptive radiation, unless perhaps it colonises a new region with many empty niches.

However, it is not true that all specialization of structure involves restriction of function. The remarkable specialization of the teeth and jaws found in the rodents enables them to deal with both hard and soft food. In this example perhaps it would be better to say that a singularity of structure has a generalized function. If all mammals had only a single digit on each limb, with but one exception and that had five by secondary multiplication, it would be called specialized, being aberrant from the usual construction, but it would be better called a singularity or peculiarity to express this fact. Mere singularity tells us nothing about evolutionary potentiality ; the lung fishes must have seemed a most aberrant specialisation to the other fishes of their age, but they gave rise to the tetrapods. Marked restriction of function, however, does suggest that the forms showing the structure causing it, if certainly not distantly related, form a monophyletic group, and may well not have given rise to anything other than more extreme forms of the same sort.

Those characters in two forms which are different but appear on functional analysis to be responses to the same functional or ecological demand are good indicators that the two forms are not closely related, and probably not derivable one from the other. For example, stridulating organs are found in very different insects, sometimes on the hind-legs, sometimes on the wings, or between the thorax and abdomen. When one set has evolved, it seems unlikely that a different set will also be produced and then the first set will be lost. It is more likely that the different sets are independent productions in different phyletic lines.

This conclusion is strengthened in those examples in which passing from one condition to another would involve going through a less adapted phase.

For instance, if the possession of an external auditory meatus formed from the ectotympanic in tarsiers and higher primates, and of a ring-like ectotympanic sunk within the bulla in lemurs, are both (in part at least) to protect the tympanum, then to pass from the lemurine to the anthropoid condition would probably involve a less adapted phase while the ectotympanic was being exserted from the bulla and the tympanum was consequently more exposed to damage, before the ectotympanic lengthened into a tube. Consequently, it is unlikely that the lemurine condition was ancestral to that in the higher primates, and far more likely that both are derived from a common form. However, this conclusion is based on the assumption that the two conditions are not also serving purposes other than protection, in which case the lemurine condition might be more efficient functionally for the modes of life of lemurs, while the other condition is actually better for the higher primates. Consequently, unless we can be satisfied that we have a fairly complete ecological and functional analysis, the conclusion cannot be certain ; but in general it can be said that no attempt to return to a less well adapted condition will succeed, because of the pressure of competition within the species and from related forms, except that in those unusual cases where a form invades an empty territory, a particular adaptation may be no longer of consequence and may be lost.

Lastly, when a condition can be shown, either on functional analysis, or by consideration of the variety of niches in which animals with it are found, to be a general improvement, rather than an adaptation to special circumstances, it acquires particular importance phyletically. It is unlikely that such general improvements will be lost ; consequently, forms with them can be derived from related forms without them, but hardly vice versa. By a general improvement is not meant necessarily one of universal application, but one which gives its possessor the potentiality of spreading into a number of different niches, not one which specializes it more efficiently for one niche. The acquisition by one form of a general improvement (very often a homoeostatic mechanism) may, and probably usually does, mean that this form undergoes radiation, extinguishing a number of forms less well adapted. However, some few pre-existing forms may persist in face of it because, being already highly specialized for particular niches, each can occupy its own niche so efficiently as to prevent the new and spreading form from approaching it and thereby acquiring the particular specializations appropriate to it. Probably the persistence of the platypus and echidna in Australasia, in face of the marsupials, is an example of this. Rarely, the new form may be hardly able to spread until a large group of highly specialized but less improved forms has become extinct from some cause or other. This seems to be one of the factors that prevented much radiation in the mammals before the extinction of so many reptiles at the end of the Cretaceous.

The possession of a general improvement by one group of animals does not of course mean that some unrelated group without this particular feature is less well adapted to its mode of life. In fact, the persistence of large groups of many diverse sorts of animal is in itself the indication that these great groups are better adapted to their particular modes of life than is the one which

has acquired an improvement but has been unable to oust them. Even though the vertebrates have improved their organization progressively, the protozoa have not become extinct. They remain at the present day the best adapted for protozoan modes of life, and have not been ousted by mammals. On a smaller scale, the cetaceans have all the mammalian improvements, and no doubt were responsible, on their rise, for the extinction of a number of marine vertebrates, but they have not completely replaced the teleost fishes, which themselves have not extinguished the selachians, and both these latter groups must be well enough adapted for their modes of life to coexist successfully at the present day with the cetaceans.

The possession of a general improvement does not mean, either, that it cannot ever be lost. The parasitic members of so many phyla show that almost everything can be sacrificed to a mode of life with stringent requirements. But within the domain of the mode of life for which a particular condition is a general improvement, it is not likely to be lost. It would not be surprising if *Myxine* were to go on in its present trend so far as to become an internal parasite and lose all the main vertebrate characters ; but it would be surprising if we were to find a mammal which had reverted to a reptilian type of brain while continuing to lead a non-parasitic life.

(b) *Genetic inertia*

It is obvious that we do not see in our own lifetime widely separate forms transforming into one another. Organisms take time to evolve, and this is, in part at least, because of genetic inertia. A violent selective pressure may be applied to a population, which will then respond by producing a change in the appropriate structure ; but unless that changed structure is suitably related to the rest of the genotype and phenotype, viability and fertility may fall disastrously. Mather & Harrison (1949), for example, have demonstrated just such a decrease in fertility when selecting *Drosophila* for an apparently very trivial character-change in chaetotaxy. Organisms are—indeed must be—highly integrated wholes, and no great change can be produced in one part without corresponding adjustment in all the others involved with it in any way (genetically, structurally, physiologically or ecologically). When the change requires a definite sequence of minor changes, the actual relative times of the changes must also be right. Consequently, the successful establishment of any considerable change may mean selection of different allelomorphs at many loci, and the recombination of at least as many others. This will take some time, unless an infinite population is available for selection to work on, since lack of particular allelomorphs, the necessity of breaking up some linkage groups, and the production of many unwanted combinations by random mating will all slow down the process.

How powerful genetic inertia is in reducing the possible rate of transformation of a given population seems not to be known. We can all agree that mice cannot be transformed into men in ten generations. But whether it is a serious limiter in large populations with annual, or more frequent, generations over a period of ten million years is another matter. Evolution as Simpson (1951 b) especially has pointed out, is *ad hoc*. Different stocks respond to what

opportunities come their way, so that adaptive radiation and convergence are rife. This strongly suggests that over long periods genetic inertia is not of great importance. But what is a long period in this context is not yet determined. It is true that in the few examples of speciation or subspeciation that can be dated approximately, it has taken thousands of years to produce really rather trivial differences ; but in none of these is there any indication that the separated populations have experienced large and divergent selective pressures. Observed rates of change may be far smaller than possible ones ; a line may be changing very slowly not because of genetic inertia but because of stabilising selection (Schmalhausen 1949, Waddington 1957), and if it now colonises a new area, it may evolve for some time at a far greater rate. In general, a very slow rate of evolution may be the result of a delicate balance between enormous forces, as Haldane (1954) has emphasized.

Nevertheless, the argument has been used that two related forms occur too close together in time for one to have given rise to the other. Consequently one must have persisted for a long time during which a population that had separated from it was slowly transforming into the other form. This argument has been used, very reasonably, with the South African australopithecines (see p. 9 above). But unless the two forms are very different and nearly or quite contemporary, the argument is of uncertain value.

A more frequent form of the argument from genetic inertia is used when the genetic basis of a character is known to be simple. If a character, however striking, or a complex of characters, however numerous and diverse its constituents, can be shown to be controlled by a single allelomorph, there is a widespread feeling that it can change very readily by mutation and therefore is highly untrustworthy as an indicator of phyletic relationship, since forms without it may be closely allied to others with it. Conversely a black mutant is known from many species of moth which are not themselves closely related. It has the effect of blotting out a complex pattern, and so causes changes in many characters ; nevertheless if it can arise independently in many different stocks, no reliance can be placed upon it, and although the products may resemble each other more in colour than they do their own original stocks, one cannot group them together phyletically. It has too little genetic inertia, and is blown about, so to speak, at random by the winds of chance.

(Such a mutant is often considered unimportant on quite different grounds, namely because it cannot point to biospecific distinctness. For example, there is a blackish race of the barking pigeon *Ducula rosacea*, which inhabits Christmas Island. It looks very different from the other races, and even in the latest revision (Peters 1937) it is regarded as a full species, *D. whartoni*. But such melanistic forms occur widely in birds as individual variants, probably because of a single gene differerence ; consequently one feels that even so striking a character probably does not mean that its possessor could not interbreed freely with the other races of *rosacea*, were it to meet them, and the difference is not important bio-specifically. This reason for unimportance must not be confused with that given just above.)

However, as Darwin pointed out in the ' Origin ', an occasional mutant form (e.g. those with stripes in horses) may give a valuable clue to ancestry.

However fleeting and sporadic a character may be, if it serves to link one group with another in such a way that convergence is not suspected, it may be of great importance in suggesting what lines to draw between given forms. The same character can be of the highest importance for one taxonomic purpose, and of none at all for another ; but it is fatal to let its unimportance for one purpose colour one's view of it for other purposes. Yet this is often done.

(c) *Intra-superspecific variation*

Quite irrespective of whether anything at all is known or even suspected about the genetic basis of a given variation, the discovery that it occurs within a single life-history, among the progeny of a single parent, as an individual variant within a single intra-breeding population, or in a single geographically separated population which on other evidence can have acquired its distinctiveness only recently (i.e. is still within a superspecies) suggests immediately that it can vary too readily to be useful phyletically. A study of such variation may suggest phyletic connections previously unsuspected.

For example, in the lories of the genus *Trichoglossus* (reviewed by Cain 1955) the upper parts except the head are mostly that brilliant iridescent green common in the group of parrots generally. In one subspecies alone, the green areas are in some individuals tinged with a bronzy yellow, in others they are strongly suffused with it, and in yet others, this colour completely supersedes the green wherever it occurs in the plumage. This is a surprising and nearly unique variation in the lories, but its mode of occurrence suggests that no great difficulty was overcome in producing it, and perhaps no lengthy period of time was necessary. One of us (A.J.C.) has preserved in an alcohol-glycerine fluid specimens of a different race of *Trichoglossus haematodus*, which have gradually developed exactly this bronzing on all their green feathers ; but washing and drying a feather restores the green to it. It seems that all that has happened is the partial or complete obliteration of the structural blue colour on their surfaces, so that a yellowish carotenoid within the feather, which normally combines its visual effect with the structural blue to make iridiscent green, is now seen by itself. This observation tends to confirm the suggestion that the bronzed individuals in the Admiralties and New Hanover, although striking and unique in the group, could have been produced by a very slight change from normal *Trichoglossus*.

CLASSES OF INFORMATION FOR PARTICULAR ACTIVITIES

From the foregoing survey of evidence that has been used in making phyletic arrangements, we can now see why there has often been much dispute over the interpretation of acknowledged facts in the past. The classes of evidence are diverse, their possible combinations numerous (probably not all have been surveyed above), and their modes of employment so different that there is scope for almost unlimited misunderstanding, the more so since phyletic interpretation is often set out using such expressions as " true affinity " or " real relationship " or " important " with very undefined meanings.

We can now summarize the available sorts of evidence in relation to the different activities distinguished above.

(i) *Relevance of evidence*

All evidence from function and ecology must first be examined to see whether any characters are, or are likely to be, necessary correlates. If they are, then all but one of them must be disregarded in all phyletic comparisons involving any of the forms that carry them. Which one is retained is immaterial from this point of view, and might be that one most easily measured, or most likely to be recognizable on incomplete material. In general it will always be safer to use the one that gives the greatest difference between the forms concerned, since this reduces the danger of overestimating their closeness of relationship. It must be repeated that the mere observation that some characters are correlated is not sufficient for them to be disregarded.

(ii) *Patristic affinity*

When all irrelevant evidence has been rejected, the remaining characters of the forms under examination are the raw material for distinguishing between convergent and patristic similarity. This must be done when only comparative data are available, and to do it we must group the forms on their remaining characters, and scan the groups so formed to find convergent characters. Then any part of the resemblance shown by two groups that is provided by their having convergent characters in common must be disregarded when we are constructing patristic groups. However, when either of these groups is being compared with another which has no convergent similarity with it (as far as we know), the characters convergent with those in the other group, disregarded in that comparison, need not now be discarded.

For example whales are not placed closest of all the mammalian orders to the fishes. Their points of resemblance are convergent and are therefore disregarded in that comparison. But if we want to know how different the Cetacea are from the rest of the Mammalia (in estimating their taxonomic rank, or the degree of diversity within the Cetacea, or in finding the closest relatives of the Mammalia) these characters are of course not disregarded, since they help to show the direction and degree of divergence characterizing the Cetacea within the Mammalia. Convergent characters, therefore, are disregarded when patristic similarity is to be found, but only in comparisons between the convergent groups.

All further evidence, besides the purely comparative, must now be examined to reveal any additional examples of convergence. If convergence is suggested by any absolute or relative dating, any combination of time, geology and geography, any functional or ecological analysis, then again, the characters concerned must be disregarded in that comparison which involves both the forms or groups concerned. If disjunct distributions suggest convergence, then further data must be obtained to test the point.

When all the possible corrections for convergence have been made, we have the data to make up patristic groups (as far as our evidence allows us) by the same method of comparison as in a phenetic classification (Cain & Harrison 1958).

(iii) *Cladistic affinity*

The foregoing activities will very likely suggest how some at least of the corrected groupings now established should be connected by phyletic lines, especially if there is some fossil evidence to work on. For example, the mere phenetic grouping of a sufficient number of forms may indicate some lines ; or the anatomical topology may show that one form could not have been derived directly from another. But there are additional sources of information on what lines should be drawn to connect groups the intermediates between which are not actually known. Time of occurrence (relative or absolute) may suggest which way round a series of forms should be read. Functional or ecological analysis may reveal general improvements, unlikely to be lost when once acquired, except for special reasons. Functional trends, in a group undergoing strong adaptive radiation may suggest a connection between specialized forms and some particular relatively unspecialized one. A change from a particular specialization which would involve passage through a less adapted phase is unlikely to take place in a rich biota. Where an apparently complex difference in many characters can be ascribed to selection resulting from a simple change of niche, we realise that this change could take place quite rapidly. The time of appearance of a niche may determine the appearance of particular forms (e.g. land tetrapods could not evolve before terrestrial vegetation). Lastly, genetic inertia may be thought too strong to allow one known form to have transformed into another, and this warns us not to draw a line directly between them at their known times of occurrence. However, since one of them may be a persistent primitive type, the phyletic line may still be drawn from one to the other after all ; we are now dealing with the problem of fitting the evolutionary dendrite when obtained to a definite time scale, rather than with that of constructing the dendrite itself.

Drawing in the most probable phyletic connections between the known forms will give us some information on relative times of divergence. More will be got from absolute or relative datings. We are then in a position to say something about actual rates of evolution, which in themselves may suggest further phyletic connections. A stage very rapidly passed through may conceivably have persisted unchanged elsewhere, but it might be worth considering whether an apparent survivor not completely identical with the rapidly superseded form is not really convergent upon it. An "early" *Gryphaea* found very late in the Mesozoic, for example, is more likely to belong to a late development of the Gryphaea-type from the Ostrea-type, than to be a survivor from an *Ostrea* line that developed the Gryphaea-type characters to the full far earlier.

Apart from this, however, it might be thought that absolute datings or actual rates of change are matter for the evolutionist rather than the taxonomist, like questions of competition and extinction arising out of the recognition of convergence. One doubts whether any New Systematist would wish to exclude them from his studies.

(iv) *Enigmatic characters*

There may well be characters observable on the forms under examination, about which we are completely in the dark as to whether they are likely to

show convergence or not, whether they are of cladistic value, and what is their functional and ecological significance. This will happen especially in very imperfectly known groups, containing at present only a few very scattered and diverse forms which show no trends, and in groups of unknown ecology showing enigmatic structures. The significance for a phyletic arrangement of such characters and their similarities in different forms is wholly unknown, and therefore they can be of no use in this activity. Consequently they can be disregarded. All the characters observable in some groups must be disregarded, and this is right, since what we are saying in effect is that we can have a phenetic arrangement of such a group but have no clue to its actual phylogeny.

(v) *Common ancestors*

When the groups recognized have been corrected as far as possible to monophylety, and the most probably phyletic connections between them have been drawn in, we can say what common ancestors of groups are missing If we want to, we can try to reconstruct them. There is no point in doing so until now, when all possible evidence has been taken into account. The methods available for doing so, however, are not very satisfactory.

Since we cannot tell from comparative data only, what examples of convergence have been concealed by even the corrected phenetic arrangement of an imperfectly known group, all we can use is Occam's razor ; certainly the simplest assumption is that the groups recognizable are monophyletic groups, each with a common ancestor. But in the first place it must be noted that the procedure of abstracting from a phenetic group all those characters which are found throughout it, or nearly throughout it, and regarding them as primitive, necessarily gives us less and less information about the presumed ancestor as the rank of the group they were abstracted from is higher in the taxonomic hierarchy, and the diversity contained within it is greater. Often, no doubt, this procedure does have the effects of removing from consideration various subsequent specializations. A primitive annelid may perhaps have consisted of a prostomium, pygidium, and a large number of virtually identified metameres between, all carrying identical parapodia. Similarly, the most primitive vertebrate may have had the simplest segmentation possible. But some of the abstractions thus produced seem so simplified and abstract as to make us wonder if they could ever have survived as actual animals. Each ancestor must have actually existed and persisted ; it cannot have been merely a rarefaction of later forms.

In the second place, it may well be that the common ancestor of a given group did not have all the characters common to or general in that group. It may have had features of its own, since lost in its descendants ; it may have been intermediate between all the extant forms in only some characters ; or indeed it may even have been identical with a known form, whose peculiarities, ruled out if only common or general characters are to be considered, are really the indication of this line's having persisted unchanged. The method of common or general characters will often lead us to postulate ancestors that never in fact existed, even although it may have happened to work well in a

few instances (e.g. *Amphioxus*), and to look in the wrong direction for missing links, which we will therefore fail to discover. Why then has the method been so popular ?

The main reason for this is simply that it has sanctioned in evolutionary terms a procedure of high repute in pre-evolutionary taxonomy, and that this procedure has therefore been uncritically taken over and maintained. By abstracting from a natural group all its common characters, one simultaneously constructs a definition by which to identify all its members as belonging to the group and to decide on the fitness of forms discovered later to be members of it, and one states the generalisations that can be made about the group. These provide succinct statements that need not be repeated for each member of the group, so that a systematic exposition of the forms concerned can be made as concise and easy to use for reference as possible. By a simple but unfortunate mistake, the definition so made was regarded as the essence of the group, the things that make it what it is, without which it could not exist (Cain 1958), the features of supreme importance, all others found in only one or a few forms being mere accidents in the strict sense of the term. With the advent of evolutionary theory, this " all-important " set of characters became those which the group owed to its common ancestor, and therefore still of overriding importance in tracing its evolution. But, as said just above, this is true only if there has been nothing but divergence in every group. The example constructed by Darwin in the ' Origin ' does in fact take into account only divergence (which is what he was chiefly concerned to explain) and persistence unchanged, and he did not consider convergence with the same thoroughness.

The common ancestor as so constructed is in fact not a common ancestor at all but an archetype as understood by Richard Owen and others of the Naturphilosophen. It is an abstract of the general plan on which a group may be considered to be modelled, and being obtained only by abstraction from the known forms, may differ considerably from the actual common ancestor.

PROCEDURE

In a previous paper (Cain & Harrison 1958) we have given an analysis of the taxonomist's judgment of overall affinity (irrespective of phyletic weighting) and a procedure for expressing the degree of phenetic affinity numerically. The analysis in the present paper of what is involved in phyletic weighting allows us to show the relations between the two, and to express the weighting precisely also.

In the procedure for phenetic affinity, all available characters of the forms to be compared are measured in all the forms. The various values for each of the characters are then divided by the maximum value observed for that character. By doing this, the actual units of measurement are removed and the values of all the different characters are brought to the same scale. The reduced values, which, as in the dummy example shown in Table 1, are conveniently expressed as percentages, can, therefore, be used for determining overall differences. Each form is compared with every other form for each of

the characters separately as in Table 2. All the differences between any two forms are then summed and the total difference divided by the number of characters involved in the comparison. This yields the mean character difference (M.C.D.) which when subtracted from 1 (or 100) expresses the

TABLE 1

Characters	Forms				
	A	B	C	D	E
(1)	100	95	95	5	5
(2)	80	100	75	10	5
(3)	2	3	2	90	100
(4)	75	80	100	10	10
(5)	80	100	90	5	10
(6)	100	90	80	8	8
(7)	30	80	100	5	5
(8)	5	100	90	5	5
(9)	50	90	100	20	25
(10)	10	100	80	15	20

TABLE 2

	Differences									
	AB	AC	AD	AE	BC	BD	BE	CD	CE	DE
(1)	5	5	95	95	0	90	90	90	90	0
(2)	20	15	70	75	25	90	95	65	70	5
(3)	1	0	88	98	1	87	97	88	98	10
(4)	5	25	65	65	20	70	70	90	90	0
(5)	20	10	75	70	10	95	90	85	80	5
(6)	10	20	92	92	10	82	82	72	72	0
(7)	50	70	25	25	20	75	75	95	95	0
(8)	95	85	0	0	10	95	95	85	85	0
(9)	40	50	30	25	10	70	65	80	75	5
(10)	90	70	5	10	20	85	80	65	60	5
Phenetic difference (=M.C.D.)	33·6	35·0	54·5	55·5	12·6	83·9	83·9	81·5	81·5	4·0
Phyletic difference	68·7	68·7	54·5	55·5	12·6	83·9	83·9	81·5	81·5	4·0

degree of phenetic affinity of the two forms. Now, it is clear from the analysis given in the present paper, that the first correction needed in converting a phenetic to a phyletic comparison is to exclude from the analysis all necessary correlates, since these give us no information on convergence or patristic affinity. Where in a complex of characters some are necessary correlates and others are not, only the second sort can be used. If it is difficult to disentangle what components are free and what necessarily correlated, it may be safer to omit the whole complex as of doubtful value. Next, to make as sure as possible that we are dealing with patristic groups, as against merely phenetic ones in which not all possible allowance has been made for convergence, we simply remove from the comparison all the characters believed or known to be convergent between the forms or groups compared. All

similarities in characters for which we have no information one way or the other as to whether they are patristic, can also be removed, in comparing the similar forms. But all differences can be left in. This reduces the number of characters compared in these particular comparisons only, which as was seen from the examples of whales and fishes is what is in fact done. Thus, for instance, if we decide in our dummy example that characters 1 to 6 show convergence in form A on B and C, we must disregard these characters when comparing A with B and C, and the corrected affinity (patristic affinity) differs as shown. A is then seen to be rather closer to D and E than to B and C.

However, although at this stage we have produced patristic groups, these do not necessarily tell us anything about how the forms with such groups were connected phyletically, nor from what forms within them were derived others that have evolved further and lost the primitive characters. These connections, if discernible at all, we obtain by looking not at the characters giving patristic affinity but only at those characters or comparisons recognized as giving cladistic information on the criteria given above, and to do this we must disregard the former.

The additional procedure necessary for converting the phenetic affinity table into phyletic one, therefore, is simple.

(a) Remove all enigmatic characters, unless so complex that their complexity suggests monophylety.

(b) Remove from the affinity table all but one of any complex of characters which is functionally or ecologically necessarily related.

(c) Make up the difference table, discarding all differences between characters which on the sorts of evidence set out above are convergent or are likely to be convergent.

(d) The modified values of overall difference so obtained are the best from which to construct patristic groups. This is an important stage for the taxonomist who wishes to delimit and name groups.

(e) Lastly, one works through the list of characters in the table, discarding all those that give only patristic affinity. The remainder, which give cladistic information, are now used to regroup the forms to give the most probable phyletic lines.

Finally, if it is thought desirable, the probable common ancestors of the groups now recognized can be constructed by the methods of common characters or extrapolation.

DISCUSSION

The procedure just given makes clear the differences between a plain comparison of phenetic affinity (overall similarity) and a phyletic comparison starting from the same data but weighting for phyletic relationship. The second comparison is so usual in modern taxonomy that it takes something of an effort to disentangle it in one's thinking from the simple comparison of overall similarity such as is used to express the actual amount of similarity (or difference) between two or more forms.

The analysis of evidence for phyletic weighting makes clear the complicated role which various classes of evidence play. Function for example, enters (a) to remove useless data (b) in conjunction with ecology to indicate likelihood of change, and (c) to identify primitive members of an imperfectly known line

of specialization. Time gives the actual direction of evolution of a known series, and indicates some evidence of convergence. To say that a particular class of evidence is important, therefore, is vague. Phyletic weighting includes several activities, and one class of evidence may be important for more than one of them.

Strictly speaking, we cannot test the reliability of any attempt at tracing phylogenies from imperfect material except by discovering further forms. However, as already remarked, there is one important principle in scientific hypothesizing which can, and must, be invoked. This is Occam's razor. If it is not used we are importing unwarranted speculations into our work. These, as we know from experience, are far more likely to be wrong than right ; it is seldom that anyone hits upon a highly particular truth by pure unsupported guess. Consequently the most suitable hypothesis to be used in filling up a gap in the fossil record is the simplest. It must be pointed out that this does *not* mean that the simplest hypothesis is always the correct one, but only that in the absence of all other evidence or rules to guide us, it is the most expedient scientifically. It might well be argued however, that the, evidence is not such as to bear any hypothesis. Those who feel that in such circumstances no hypothesis should be put forward must restrict themselves to the phenetic classification ; those who feel that since the doctrine of evolution is so firmly based, any classification should be as consistent with it as the taxonomist can contrive, must use the enigmatic characters, but must proceed with Occam's razor in hand. If, as well may happen, they encounter a situation in which two or more equally simple hypotheses can be put forward, they too must be content with a phenetic classification of the entities involved.

A remarkable feature of the weighting as described above is that it is all-or-none. A character is either left in for a given comparison or it is struck out. At first sight, this is surprising ; surely there are degrees of reliability, and it might be thought a serious objection to the procedure that it allows no place for them. One character might vary considerably in a group and so be regarded as less likely than a more constant one to be truly primitive. Or evidence other than comparative might make it seem more probable that one character, rather than some other, is liable to convergence, or actually shows it, in a given group. But either the character is primitive or it is not ; either it did occur in the common ancestor or its immediate descendants (or appeared in a certain degree of development) or it did not. We can hardly put in half a character if we are unsure. The degrees of uncertainty, therefore, are as to whether the character (or a particular value of it) is to be included in the list of relevant characters for a given comparison, or whether it is to be excluded ; and it may be entirely a matter of opinion as to whether it should or should not, and equally a matter of opinion as to what level of probability should be used. This is where the greatest uncertainty is found in phyletic weighting and unless a definite probability can be stated (as when convergence is conclusively demonstrated) the uncertainty is not removable. The probability may be practically unmeasurable, and if opinions differ, the only course is to work the tables once with and once without the doubtful characters and show both the end results. Taxonomists often say of an imperfectly known form

that it may or may not have had a given character ; this corresponds exactly to the procedure just recommended, for its overall affinities or phyletic affinities will differ to that extent according to which possibility is accepted for further argument.

Covariation of characters was emphasized by Darwin in the ' Origin ' as of great taxonomic importance. But importance, as already mentioned, is too vague a word in such discussions without a statement of the purposes for which the entity must be considered important. In fact, Darwin says " Numerous instances could be given of characters derived from parts which must be considered of very trifling physiological importance, but which are universally admitted as highly serviceable in the definition of whole groups ". And " The importance for classification, of trifling characters, mainly depends on their being correlated with several other characters of more or less importance. The value indeed of an aggregate of characters is very evident in natural history. Hence, as has often been remarked, a species may depart from its allies in several characters, both of high physiological importance and of almost universal prevalence, and yet leave us in no doubt where it should be ranked." And " Practically when naturalists are at work, they do not trouble themselves about the physiological value of the characters which they use in defining a group, or in allocating any particular species. If they find a character nearly uniform, and common to a great number of forms, and not common to others, they use it as one of high value ; if common to some lesser number, they use it as of subordinate value . . . If certain characters are always found correlated with others, though no apparent bond of connexion can be discovered between them, especial value is set upon them." And " We care not how trifling a character may be—let it be the mere inflection of the angle of the jaw, the manner in which an insect's wing is folded, whether the skin be covered by hair or feathers—if it prevail throughout many and different species, especially those having very different habits of life, it assumes high value ; for we can account for its presence in so many forms with such different habits, only by its inheritance from a common parent. We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, occur together throughout a large group of beings having different habits, we may feel almost sure, on the theory of descent, that these characters have been inherited from some common ancestor. And we know that such correlated or aggregated characters have especial value in classification."

These quotations are from the 13th chapter of the ' Origin '. They are of particular interest here because they show what importance should be attributed to the correlation of characters in a non-evolutionary taxonomy, and what change was made by the author of evolutionary theory. The non-evolutionary importance is simply that such correlated characters are the best for *defining* a group, and for *identifying* the members of it. And they serve in *constructing phenetic groups*, since by their aid we avoid the pitfalls of one-character classifications. But in an evolutionary classification, they are taken to indicate *phyletic relationship* provided they are functionally independent characters (" no apparent bond of connexion can be found

between them "). But it will be seen from the quotation given third above, that the different degrees of importance given to a character which occurs in many forms (which themselves must be a patristic group, of course, otherwise it will have to be rejected as convergent in some of them) as against one which occurs in few, are primarily hierarchical ; the former helps to define a high rank for the group, the latter only a lesser one. This interpretation is strengthened by the example Darwin gives from Westwood, that in the Hymenoptera, in one great division the antennae " are most constant in structure ; in another division they differ much, and the differences are of quite subordinate value in classification. . . ." Similarly, in the example Darwin takes from Robert Brown, characters which otherwise are of *generic* importance are insufficient to separate two *genera* of Connaraceae. And earlier in the same paragraph Darwin says " That the mere physiological importance of an organ does not determine its classificatory value, is almost shown by the one fact, that in allied groups, in which the same organ, as we have every reason to suppose, has nearly the same physiological value, its classificatory value is widely different ". It seems, therefore, that the degree of importance or the classificatory value in this connection refers not to the help given in framing a definition, nor in identifying a form as a member of a particular group, but to the *rank* of the group definable by it. In fact, Darwin does not discuss the value of characters sporadically distributed within a patristic group, except in dealing with reversion in the chapter on Laws of Variation, where he indicates plainly the value of a reversion in the construction of a common ancestor. His general discussion of classification is founded on the classification as accepted by taxonomists in his own day, and this automatically disregarded highly variable or sporadic characters.

It seems, then, that Darwin also would have disregarded highly variable characters for the purposes of classification, unless they could be shown to be reversions. But a character which appears once only among the members of a group known only from living forms may perhaps have existed in the common ancestor. Is it generally thought that a character which occurs in only half the forms (and not so distributed that it defines a phenetic sub-group) is half as likely to be ancestral as one occurring in all ? If so, one must make up one's mind as to whether it is to be taken as ancestral or not, and again we come back to leaving it in the appropriate comparisons or striking it out ; we can hardly put it in with only half its value. Consequently we can say that the weighting, on the procedure given in this paper, for phyletic affinity must be all-or-none, and there is certain to be some difference of opinion as to what should and what should not be included.

The difference between estimating phenetic affinity to determine the diversity within a group and so the taxonomic rank it should have, and estimating phyletic affinity and therefore which groups should be regarded as closest cladistically, has not always been fully realized. For example, in Mayr's excellent review of the birds of paradise (1941) it is shown that although different species differ very greatly in their plumage, far more than do species in other groups of birds which are always placed in different genera or even subfamilies, they may hybridize, even rather frequently. Mayr rightly takes

this as evidence that although apparently different, these forms are genetically similar. Therefore they should not be put into separate genera. But if in fact the forms concerned do differ overall more than do many others which are put into different genera, then they also must be in different genera ; whether the differences were acquired rapidly or recently is immaterial. The only good grounds for combining the forms in one genus would be if the genetic bases of the differences were so slight that their simplicity completely overweighed the complexity of the plumage and behavioural differences in a straightforward comparison of affinity. But such a comparison has not been made precisely yet. And moreover, it is always possible to say that the simplicity of the genetic differences is due to a very complex adjustment of the rest of the genotype ; but in this example the production of viable (though probably sterile) hybrids is taken as a general index of similarity of the genotypes, not of the complexity of the genetic bases of the differences. However, we do not know just how similar two forms must be to produce hybrids at all, and we do know that these forms are morphologically more different than those usually included by ornithologists in the same genus. (It is no part of the purpose of this paper to decide whether their criteria should be altered.)

A feature of the analysis of phyletic weighting presented here is that it emphasizes the very doubtful value of constructing common ancestors unless the fossil evidence is reasonably good. The extrapolation backwards in time of several well-known fossil lines, because it is based on a great deal of evidence, may give a good approximation to the actual common ancestor, confirmed by subsequent discoveries ; but the assumption of constant rates of divergence as applied to a group known only from living forms may be most seriously misleading, as Bigelow particularly has stressed. Where a phenetic group is characterized by a large number of characters and functional analysis relates them to one mode of life, we may well feel that it is also a monophyletic group, but as shown above, the possibilities of convergence from fairly closely related ancestral stocks cannot be ruled out—indeed all functional analysis opens our eyes to additional possibilities of convergence. It is far better to label such groups as phenetic ; they are still the most useful for most purposes, even if we cannot be sure that they are monophyletic. Certainly the worst thing is to decide beforehand what characters must be more important, and classify the group to satisfy the principle ; yet this is still often done.

The advantages of the procedure given in this paper are that it enables us to state precisely what evidence is available for what purposes, when a phyletic arrangement is to be made, and to express the results numerically if desired. This should avoid a great deal of ambiguity and misunderstanding.

ACKNOWLEDGMENTS

We have greatly profited by criticism of this paper kindly given us by Professor Sir Wilfred Le Gros Clark, F.R.S., Dr N. Tinbergen, Dr J. M. Cullen, Dr F. Hall, Mr J. S. L. Gilmour, Mr H. K. Pusey, Mr B. C. Clark, Mr J. D. Currey, and Mr K. A. Reynolds, all of whom read the earlier version in detail.

SUMMARY

1. In the making of a phyletic arrangement several different activities are involved.
2. These include testing phenetic groups for monophylety, drawing the most probable phyletic connections between them, and (if desired) the partial reconstruction of common ancestors.
3. The evidence relevant is of various sorts, and any one sort can be relevant in different ways for more than one of these activities. Functional analysis, in particular, is shown to play a very complicated part.
4. The results are expressed in a definite procedure for phyletic weighting, which reduces ambiguity and imprecision considerably.
5. It is emphasized that many groups are best left as phenetic (" natural "), and that the construction of common ancestors, except where much evidence is available, is often of very doubtful value.
6. Darwin's procedure in the ' Origin of Species ' is shown to take too little account of the difficulties arising from convergence.

REFERENCES

Bather, A. J. (1927). Biological classification : past and future. *Quart. J. geol. Soc.* **83** : lii–civ.

Bigelow, R. (1956). Monophyletic classification and evolution. *Syst. Zool.* **5** : 145.

Bigelow, R. (1958). Classification and phylogeny. *Syst. Zool.* **7** : 49.

Cain, A. J. (1955). A revision of *Trichoglossus haematodus* and of the Australian platycercine parrots. *Ibis* **97** : 432–479.

Cain, A. J. (1958). Logic and memory in Linnaeus's system of taxonomy. *Proc. Linn. Soc. Lond.* **169** : 144.

Cain, A. J. (1959 a). The post-Linnaean development of taxonomy. *Proc. Linn. Soc. Lond.* **170** : 234.

Cain, A. J. (1959 b). Inductive and deductive method in post-Linnaean taxonomy. *Proc. Linn. Soc. Lond.* **170** : 185.

Cain, A. J. (1959 c). Function and taxonomic importance. In Publication no. 3 (Function and Taxonomic Importance), Systematics Association. London: Systematics Association.

Cain, A. J. & Harrison, G. A. (1958). An analysis of the taxonomist's judgement of affinity. *Proc. zool. Soc. Lond.* **131** : 85.

Clark, W. E. Le Gros (1955). *The fossil evidence for human evolution.* Chicago : University of Chicago Press.

Gilmour, J. S. L. (1940). Taxonomy and philosophy. In *The new systematics*, ed. J. S. Huxley. Oxford University Press.

Gilmour, J. S. L. (1952). The development of taxonomy since 1851. *Advanc. Sci.* **9** : 70.

Haldane, J. B. S. (1954). The statics of evolution. In *Evolution as a process*, ed. J. S. Huxley, A. C. Hardy and E. B. Ford. London : Allen and Unwin.

Huxley, J. S. (1959). Clades and grades. In Publication no. 3 (Function and taxonomic importance), Systematics Association. London: Systematics Association.

Mather, K. & Harrison, B. J. (1949). The manifold effect of selection. *Heredity* **3** : 1 & 131.

Mayr, E. (1941). *List of New Guinea birds.* New York: American Museum.

Mayr, E. (1942). *Systematics and the origin of species.* Columbia University Press.

Michener, C. D. & Sokal, R. R. (1957). A quantitative approach to a problem in classification. *Evolution* **11** : 130.

Oakley, K. P. (1954). Dating of the Australopithecinae of Africa. *Amer. J. phys. Anthrop.* **12** : 9.

PETERS, J. L. (1937). *Checklist of birds of the world.* **3.** Cambridge, Mass. : Harvard University Press.

SCHMALHAUSEN, I. I. (1949). *Factors of evolution.* Philadelphia : Blakiston.

SIMPSON, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Amer. Mus. nat. Hist.* **85** : 1.

SIMPSON, G. G. (1951 a). *Horses.* New York, Oxford University Press.

SIMPSON, G. G. (1951 b). *The meaning of evolution.* New York : Mentor Books.

SNEATH, P. H. A. (1957). Some thoughts on bacterial classification. *J. gen. Microbiol.* **17** : 184.

STEPHENSON, J. (1930). *The Oligochaeta.* Oxford : University Press.

WADDINGTON, C. H. (1957). *The strategy of the genes.* London : Allen and Unwin.

ZEUNER, F. E. (1958). *Dating the past.* London : Methuen.

STUDIES OF THE DIFFERENCES BETWEEN THE FAUNA OF GRAZED AND UNGRAZED GRASSLAND IN TIREE, ARGYLL

BY

J. MORTON BOYD

The Nature Conservancy, 12 Hope Terrace, Edinburgh 9.

[Accepted 10th November, 1959]

(With 1 figure in the text)

The Reef *machair* on the south side of the airfield in Tiree, Argyll is a highly uniform type of grassland which has never been tilled. The airfield was built in the locality during the 1939-45 war and the perimeter fence constitutes an ecological discontinuity of at least twelve years' standing, between grazed and ungrazed grassland. The differences in the soil fauna on either side of the fence are demonstrated by two similar batteries of pit-fall traps over a period of twelve months.

The catches of the traps consist mainly of arthropods. Over eighty species of invertebrate were identified and some of these were used for quantitative analysis. The numerical differences between catches on grazed and ungrazed plots are great, and the taxonomic groups are classified into those which are favoured by grazed and ungrazed conditions. The abundance peaks of the two plots are compared. Most of the groups have a single peak in autumn, a few in early summer and a few in both early summer and autumn. Numbers caught at times of climatic extreme are discussed. This habitat of highly uniform appearance is found to be heterogeneous and the reasons for this are given.

Fencing is an important technique in forestry and wildlife management in Britain. The finer consequences are unknown, and this paper demonstrates what these are likely to be in a simple situation in uniform natural grassland in Tiree.

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INTRODUCTION

This is a study of the differences which have evolved in twelve years in a habitat on either side of a simple ecological discontinuity. The habitat is a natural maritime grassland or *machair* as it is called in the Hebrides, grazed by cattle. The discontinuity is a cattle-proof fence. There are no rabbits (*Oryctolagus cuniculus*) in Tiree, and the survey area has been grazed by no other farm stock in the past decade. The areas on either side of the

fence were similar some twelve years previous, being part of a wide expanse of flat uniformly grazed grassland. An airfield perimeter fence was erected across it in the early years of the 1939-45 war, and now the areas are completely different. The grazed area is probably similar to the whole grassland before the fence was erected ; the ungrazed area (airfield) possesses a difference in sward, animal communities and soil structure.

One of the qualities which recommended this as an area for study was the comparative simplicity of the habitat. The site was at the airfield perimeter fence, The Reef (near Baugh), Isle of Tiree, Argyll, and is shown in previous papers (Boyd, 1957a, 1958). The system was that of a fairly homogeneous type of natural soil (which has never been cultivated in any way except by grazing) in a fairly remote island in the Inner Hebrides (vice county, Mid Ebudes 103). A visible difference had been caused in the system by the erection of the fence and it was decided to investigate this difference in terms of the monthly catches of animals in two batteries of pit-fall traps placed on either side of the fence, close enough to have been part of the same system before the fence was erected, and far enough from the fence not to be influenced by border effects. The battery on the grazed ground was the " control " and that on the ungrazed ground the " experimental."

The detailed ecology of the earthworms, as shown by the catches of these pit-fall traps, is described elsewhere (Boyd 1957b, in which the captions for Figs. 4 and 5 should be exchanged). The bulk catches of earthworms are also shown here without mention of species together with a selection of other species, genera and higher taxonomic groups caught. It is not the intention to enter into detailed ecological discussion as has been done previously with the earthworms at this site, and with four species of *Calathus* living on sand dunes in Anglesey, North Wales. The latter (Gilbert, 1956) was also done with pit-fall traps. Only a fraction of the catch is considered in this paper ; smaller forms of Diptera, Hymenoptera, Collembola and Acarina are overlooked. The fraction studied is considered adequate enough to outline the differences at a community level, the object of the survey.

METHODS AND MATERIALS

1. *In the field*

Monthly collections were made from two batteries of nine pit-fall traps (twelve traps were actually used in each battery, but shortage of time and the fact that the differences were readily apparent without the added effort, made the analysis of all the traps unnecessary). The batteries were placed about 50 m. apart, and at least 10m. from the fence. One was placed in the ungrazed and unmown grass extension at the east end of the tarmac runway, approximately in line with Baugh Cottage.

The pit-fall trap took the form of a 2lb. (0·9 kgm.) jam-jar sunk to the level of the soil surface. Each trap was set at the corner of a grid, the grid square being of 3 m. side. The traps were cleared at approximately monthly intervals (except in the periods 29th April - 18th May. 1955, and 14th January, - 12th March, 1956), and were not moved, except for clearing, from their stations, during the twelve months of trapping from April, 1955 to May, 1956. The

traps were not baited but approximately 10 cc. of strong formalin (between 10 and 20 per cent, depending on the expected rainfall) was put in each trap after clearing. The strong formalin had to be used in order that the dilution by rain would not cause the decay of the catch. Controls were set up without formalin but these were foul before they could be cleared. The apparent differences between the catches of those controls and the others were not any greater (on inspection) than those between individual traps within the batteries.

Care was taken to ensure that the lips of the traps were not contaminated with the formalin which was added with a syringe. Efforts were made to give an even turf-glass contact on the rim of the traps, but this proved difficult due to the disturbance by wind, rain and animals. Otherwise the traps were indentical.

The traps were emptied on each occasion by the author, using a standard procedure. The jar was lifted without disturbing the contents and the liquid (which on no occasion was found to fill the jar) decanted off. The decanting was done at a point some 10 m. from the battery to obviate any effect which the liquid would have on the fauna. The jar was then up-ended in the palm of the hand and the contents levered into a suitable tube with the thumb and fingers. By this method, the batteries could be cleared quickly (an important factor in inclement weather), and very few of the larger forms considered in this paper escaped collection.

The pit-fall trap method did not prove successful in obtaining catches of snails and slugs, and separate sampling was done in October using a metal quadrat of area 900 sq. cm. (1 sq. ft.) cast randomly at different stations. These quadrats were carefully worked through with forceps and all molluscs found were collected in tubes and preserved in 4 per cent formalin.

2. *In the laboratory*

The catches from the traps were brought back to the laboratory for storing and sorting, a note being made inside each tube of the serial number of the corresponding trap and the date of clearing. The dilute formalin (trap-liquid) was decanted from the tube, taking care not to lose any of the contents, and was replaced with 70 per cent alcohol. Before sorting commenced some of the catches were sent to Mr R. A. Crowson who very kindly indentified most of the species of beetle and provided type specimens from the catches as aids to identification. It was impossible in the time available to analyse other groups in such great detail as was done with the beetles (though some families such as the Orthoptera and the Dermaptera were represented by a single species), and it was found expedient merely to make a qualitative estimate of other groups by asking various authorities to name the principal species present. Again it was considered unnecessary to bring the quantitative analysis to the species or genus levels in all cases to give a sound idea of the differences between the grazed and ungrazed complexes.

Before proceeding with the counting, familiarization analyses were done and counting commenced with a sound working knowledge of all the taxonomic groups being handled. Specimens of unfamiliar beetles were sent periodically to Mr Crowson for an opinion, as the analysis progressed. The snails from

the quadrats were dried. The slugs were in poor condition when taken from the formalin and were not identified.

The number of days which elapsed between clearances of the traps varied from fifty-eight to twenty-seven, but only three were outside of twenty-seven to thirty-five. These irregularities were caused by the inaccessibility of the area from Glasgow, where the author was based at the time, and, in one instance, a visit to the survey area (in February) brought no results due to the traps being frozen solid and snow-covered. For purposes of comparison all catches are reduced to a standard of thirty days, standing and the conversions from the absolute numbers together with the conversion factors are set forth in Tables 1 and 2.

From the point of view of histogramatic illustration it is unfortunate that traps were cleared usually in the middle of the month. This has meant that values cannot be attributed to any one calendar month but to portions of two consecutive months added together. Thus the value which appears for September, for example, comprises sixteen days from September, and fifteen from October. This should be taken into account in comparing this with other data obtained from sampling at the beginning or the end of calendar months The full " monthly " data (uncorrected for time interval) are desposited with the Nature Conservancy, Edinburgh and can be supplied on request.

The nomenclature of the insects is that found in *A check list of British Insects* (Kloet & Hinks, 1945).

THE HABITAT

The site is situated on a tract of mature maritime grassland (*machair*) about 250 m. landward from a range of coastal dunes of highly calcareous shell-sand. *Machair*, by definition, contains no *Ammophila arenaria* in its swards and analysis of grazed *machair* swards in Tiree (not at the same site as this survey) show them to be dominated by *Festuca rubra*, *Trifolium repens*, *Plantago lanceolata*, *Lotus corniculatus*, *Galium verum*, *Ranunculus* spp., *Bellis perennis*, *Rhytidiadelphus squarrosus*, *Lolium perenne*, *Euphrasia officinalis*, *Holcus mollis*, *Carex flacca* (Vose, Powell & Spence, 1956). *Senecio jacobea* is present in both grazed and ungrazed swards but not in high density on the survey areas.

The ungrazed grassland has not been studied to anything approaching the same degree, but from inspection it is clear that *Festuca rubra* becomes dominant and the other species which are normally dispersed throughout the grazed swards occur only at isolated centres in the deep rank Festucetum. The *machair* is thought to be a plagio-climax maintained by grazing and that, in the event of grazing being permanently removed, it would develop into a *Calluna* or *Molinia* heath, depending on drainage. The Festucetum could, therefore, be considered as a stage in this succession.

The area in which the batteries were set up is characteristic of wide tracts of The Reef *machair* in Tiree particularly and of Hebridean *machair* generally. It is free from flooding though the rising water table causes local flooding (not on survey plots) in winter, and in the distant past it has been subject to flooding by the sea, probably on a high spring tide, assisted by a southerly gale.

The grassland is broken by a system of widely separated (c. 20 m. apart) parallel ditches probably cut at one time to relieve the area of flood waters. The soil is a 15 cm. layer of homogeneous dark brown loam on top of a deep layer of shell-sand. This layer of sand goes down to the gneiss platform, which in this locality is likely to be below sea-level, hence the name " The Reef ". It is a shell-sand vegetable mould mix of very fine grain, containing no pebbles ; a section is shown in a plate in an earlier paper on the ecology of the Lumbricidae (Boyd, 1958), and this shows the sharp discontinuity which occurs between the 15 cm. and the sand below. It has never been tilled. The pH of the soil was 7·6 to 7·7, the $CaCO_3$ content 55 to 60 per cent dry weight, the loss of weight on ignition (at 500°C for 18 hours) 11 to 15 per cent dry weight.

The wild vertebrate fauna (some of which marked with an asterisk were caught in the pit-fall traps) includes :—the long-tailed fieldmouse *(*Apodemus sylvaticus* (*hebridensis*?)), pigmy shrew* (*Sorex minutus*), lapwing (young*) (*Vanellus vanellus*), starling (*Sturnus vulagris*), gulls (*Larus* spp.), buzzard (*Buteo buteo*), golden plover (*Pluvialis apricaria*) on migration. The rabbit (*Oryctolagus cuniculus*), the mole (*Talpa europaea*) and the hedgehog (*Erinaceus europaeus*) are all absent from Tiree, but the hare (*Lepus europaeus*) is present.

The grassland of the southern aspect of The Reef is grazed from December to May inclusive and is part of the common grazings of the Crossapol crofting township. During the summer and autumn the grazed swards recover from the close-cropped condition of the spring and become ankle-deep. It follows that as the summer advances the microclimate of the grazed ground changes and this change must be taken into account when interpreting the data. The change, however, is small in comparison with the change which has taken place between the grazed swards (considered at any time of the year) and the ungrazed, and the growth of the grazed swards in summer does little to obscure this greater difference.

The climate of Tiree is maritime. The ranges of air temperature and rainfall are shown in Table 5. The island is subject to high winds, gusts of 108 m.p.h. have been recorded. The temperature range is 3·3 Centigrade degrees less than the Scottish mainland. Snow seldom lies more than a few days in the year, and the soil remains open practically all winter. Hours of sunshine are somewhat similar to those of southern England ; in May, 1948 Tiree had an average of 10·6 hours of sunshine daily (Manley, 1948).

FAUNAL ANALYSIS

Taxonomy

The material was analysed into thirty different classes containing one or more species. Such classes as do contain only one species (*Carabus granulatus*, *Nebria brevicollis*, *Notiophilus aquaticus*, *Dyschirius globosus*, *Pterostichus vulgaris*, *P. strenua*, *Calathus melanocephalus*, *C. fuscipes*, *Staphylinus aeneocephalus*, *Longitarsus jacobaeae*, *Loricera pilicornis*, *Apion apricans*, *Serica brunnea*, *Liodes dubia*, *Forficula auricularia*, *Trombidium holosericeum*, *Omocestus viridulus*) are given full specific name. Classes which are given as genera or higher taxonomic groups require a special explanation in each case :

Amara spp.	—	*A. communis, A. aenea, A. bifrons.*
Aphodius spp.	—	*A. punctatosulcatus, A. ater, A. constans.*
Xantholinus spp.	—	*X. linearis, X. cribripennis, X* (?) *glabratus.*
Tachyporus spp.	—	*T. chrysomelinus, T. hypnorum.*
Longitarsus spp.	—	*L. pratensis, L. luridus,* (*L. jacobaeae* is presented separately).
Sitona spp.	—	*S. lepidus, S. sulcifrons.*
Myrmica spp.	—	*M. rubra, M. scabrinodis.*
Opiliones	—	*Phalangium opilio, Mitopus morio.*
Araneida (spiders)	—	*Pachygnatha degeeri, Xysticus, cristatus, Centromerita concinna, Dicymbium nigrum, Ceratinella brevipes, Lophocarenum parallelum, Gonatium rubens, Silometopus elegans, Trichopterna thorelli, Hypomma bituberculatum, Erigone sp. Lepthyphantes tenuis, Cornicularia vigilax, Enoplognatha thoracica, Tiso vagans, Lycosa pullata, Lycosa monticola, Lycosa tarsalis.*
Myriopoda	—	*Cylindroiulus latestriatus, Brachyiulus pusillus.*
Tipulidae	—	*Tipula luteipennis, T. pagana, Trichyphona immaculata.*
Homoptera	—	*Aphrodes bicinctus, Deltocephalus pulicaris, Agallia venosa, Megophthalmus scanicus, Jassargus pseudocellaris.*
Lumbricidae	—	*Allolobophora caliginosa, A. chlorotica, Bimastus tenuis, Dendrobaena rubida, D. subrubicunda, D. octaedra, Eiseniella tetraedra, Lumbricus castaneus, L. rubellus, Octolasium cyaneum.*

The following were rare in the collection, were of little value in outlining the differences between plots, and were not included in the Tables : *Agriotes obscurus, Astilbus canaliculatus, Cercyon melanocephalus, Helophorus aquaticus, Gabrius* sp., *Megasternum boletophagum, Scymnus redtenbacheri, Atomaria*? *apicalis, Thanatophilus rugosus, Necrophorus humator, N. investigator, N. vespillo, Crepidodera transversa, Phytonomus plantaginis, Corymbites cupreus.*

The following species were collected in the quadrat sampling of snails : *Helicella itala, Cochlicella acuta* (not on *machair* but on adjacent dune), *Vitrina pellucida, Oxychilus alliarius, Cochlicopa lubrica, Acanthinula aculeata. Helix aspersa* and *Trichia* (*Hygromia*) *hispida* are present in the locality but were not found in the quadrats. *Cepaea nemoralis* was not found in the locality. The slugs were probably *Arion ater* and *Agriolimax* sp.

Differences between plots

The pit-fall catches probably give a fairly accurate indication of the surface activity of the soil fauna in each plot. Surface activity is an attribute which can be changed by each and a combination of the following factors : (i) additional movement of the individual, as is the case in warm dry days as opposed to cold wet ones, or vice versa, and (ii) additional individuals as at the times of hatching of eggs, pupae, and cocoons. The numbers presented have this bipartite meaning which, for want of a better term, is called " surface activity ". Since, however, both plots have been subjected to a standard sampling method which can apparently be applied with equal efficiency to both, it is at the same time indicative of the scale of difference between the animal communities at the surface of grazed and ungrazed *machair* soils particularly, and maritime soils generally.

The differences which emerged in the catches on the grazed and the ungrazed plots are, in most cases, so large as to obviate any involved statistical treatment. The numbers of animals caught in twenty-four of the thirty

classes into which the fauna was numerically analysed can conveniently be presented in histograms (Fig. 1). The numbers obtained in the remaining groups were small and can be easily read from Tables 1 and 2. In twenty-seven cases the numbers between plots are obviously different beyond the point of chance variation, and in all other cases, including those which were recorded but because of their rarity were not included in the Tables, numbers were too small to give convincing comparisons.

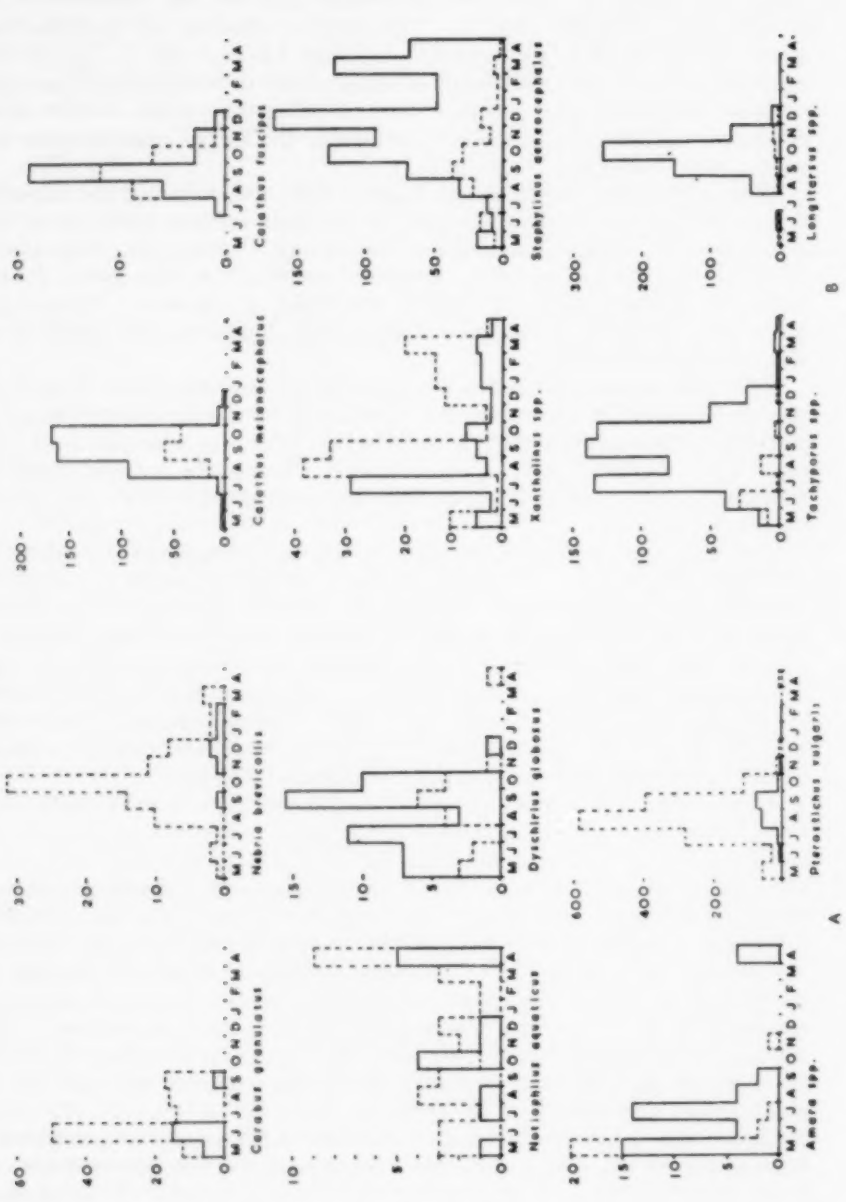
A scrutiny of the histograms and Tables 1 and 2 will show that the following groups are favoured by what are probably the more extreme conditions of the grazed ground : *Dyschirius globosus*, *Amara* spp., *Calathus* spp., *Staphylinus aeneocephalus*, *Tachyporus* spp., *Aphodius* spp (fond of dung-pats), *Longitarsus* spp. (small plants, not Fescue), (excluding *L. jacobaeae*), *Sitona* spp., *Apion apricans* (fond of legumes), *Myrmica* spp., Opiliones, Homoptera (Jassidae and Bythoscopidae).

The small chysomelid beetles, *Longitarus* spp. were numerically dominant, but the biomass of the catch was dominated by harvestmen (Opiliones), particularly *Phalangium opilio*. Such groups as *Calathus melanocephalus*, *Tachyporus* spp., *Aphodius* spp., *Longitarsus* spp., *Sitona* spp., *Apion apricans*, *Phalangium opilio* seem to be particularly favoured by conditions on the grazed grassland.

The following groups are favoured by the more temperate conditions of the ungrazed ground : *Carabus granulatus*, *Nebria brevicollis*, *Notiophilus aquaticus*, *Xantholinus* spp., *Longitarsus jacobaeae* (on *Senecio jacobaeae*) *Serica brunnea*, *Liodes dubia* (fond of subterrean fungi), *Omocestus viridulus*, spiders. The opilionids are also very numerous on the ungrazed ground, but not nearly so plentiful as in the grazed. The biomass in this case is dominated by *Pterostichus vulgaris*. *Carabus granulatus*, *Nebria brevicollis*, *Pterostichus vulgaris*, *Xantholinus* spp., *Longitursus jacobaeae* and *Serica brunnea* are particularly favoured by the conditions of the ungrazed grassland.

Of the principal species of spider caught in each battery, only one, *Pachygnatha degeeri*, seems unaffected by the fence. Other species are affected in different ways. The distribution of *Lycosa* spp. is, for instance, interesting. The analysis shows that *L. pullata* is abundant on the ungrazed ground and almost absent from the grazed. The opposite, however, is the case with *L. tarsalis* and *L. monticola*, although the males of the latter two species tend to move into the ungrazed area. *Xysticus cristatus* is much more common on the grazed than on the ungrazed ground, and a large number of immature specimens in the grazed area suggests that breeding takes place there. Concerning *Myrmica* spp., (ants), the seasonal differences between the grazed and the ungrazed plots suggests that they nest in the ungrazed and walk out on to the grazed ground early in the year.

Apart from measurements of the properties of the soil and the climate set forth in the section dealing with the habitat, and the climatic conditions of Tiree generally (Table 5), little more information is available of the physical conditions prevailing on either side of the fence. The ungrazed swards prevent the insolation of the soil surface to a much greater extent than the grazed, and the habitat at the soil surface is consistently darker and more moist in the


Carabus granulatus
Nebria brevicollis
Notiophilus aquaticus
Dyschirius globosus
Pterostichus vulgaris
Amara spp.
A
Calathus fuscipes
Calathus melanocephalus
Stephylinus caerulescephalus
Xantholinus spp.
Tachyporus spp.
Longitarsus spp.
B
M J J A S O N D J F M A

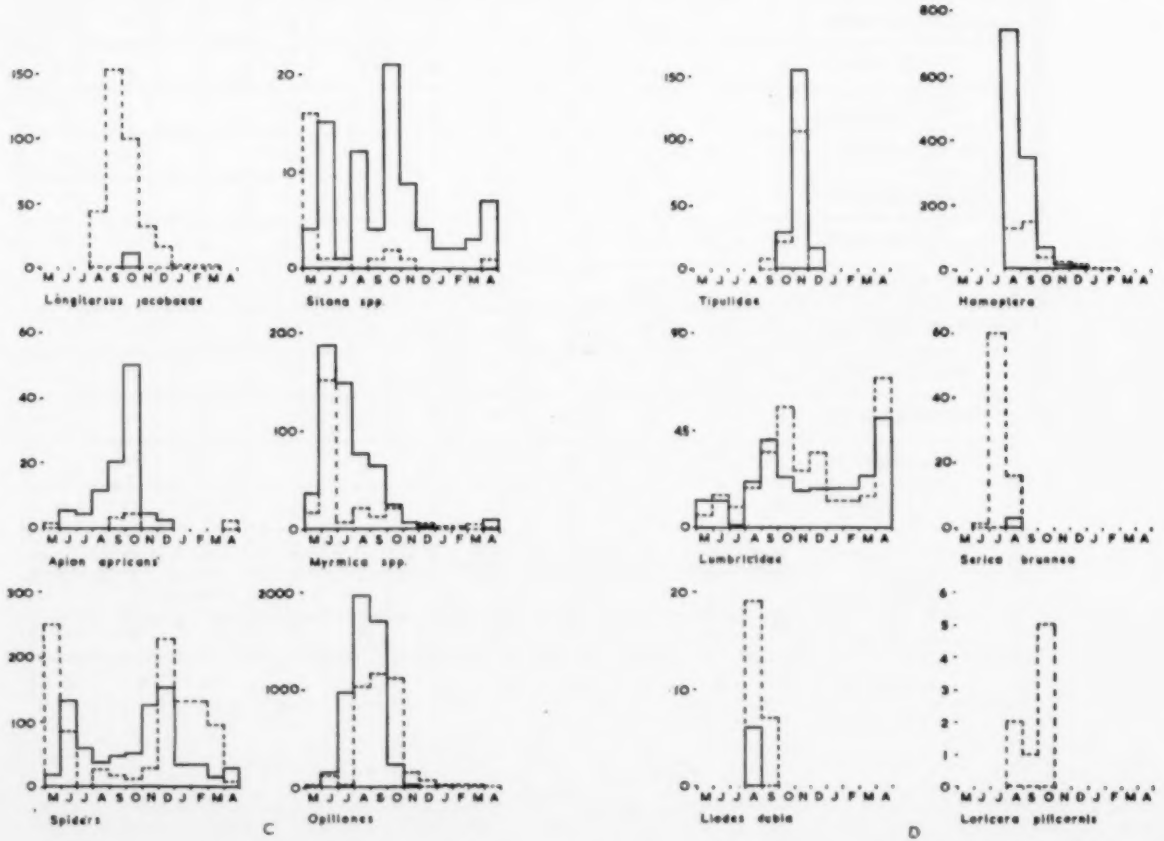


Fig. 1—Fluctuations in numbers of animals caught in the two batteries of pit-fall traps each month from May 1955 to April 1956; the continuous line denotes the GRAZED plot and the broken line the UNGRAZED.

TA

Numbers caught in the eleven periods throughout the yea

Month and Dates	Days	Conversion Factor	*Carabus granulatus*	*Nebria brevicollis*	*Notiophilus aquaticus*	*Dyschirius globosus*	*Amara* spp.	*Pterostichus vulgaris*	*Pterostichus strenua*	*Calathus melanocephalus*	*Calathus fuscipes*	*Xantholinus* spp.	*Staphylinus aeneocephalus*	*Tachyporus* spp.
May 29/4 - 18/6	50	1·7	6	—	1	7	15	1	1	2	—	5	18	15
June 18/6 - 18/7	30	1	15	—	—	7	4	3	3	2	—	2	7	39
July 18/7 - 18/8	31	1	—	—	1	11	14	5	—	6	1	29	11	134
Aug. 18/8 - 14/9	27	0·9	—	—	1	3	4	29	—	93	6	3	32	81
Sept. 14/9 - 15/10	31	1	3	1	—	16	2	37	—	161	19	5	68	140
Oct. 15/10- 11/11	27	0·9	—	—	4	10	—	8	—	167	3	7	126	131
Nov. 11/11- 14/12	33	1·1	—	1	1	—	—	1	—	5	3	2	92	50
Dec. 14/12- 14/1	31	1	—	2	1	1	—	—	—	1	1	2	165	24
Jan. / Feb. 14/1 - 12/3	58	1·9	—	1	—	—	—	1	—	—	—	4	47	1
Mar. 12/3 - 16/4	35	1·2	—	—	—	—	—	—	—	—	—	5	121	2
Apr. 16/4 31/5	45	1·5	—	—	5	—	4	—	—	—	—	2	67	1

E 1

a the GRAZED ground converted to a standard period of thirty days.

Aphodius spp.	*Longitarsus* spp.	*Longitarsus jacobaeae*	*Sitona* spp.	*Apion apricans*	*Myrmica* spp.	*Forficula auricularia*	Araneida (Spiders)	*Trombidium holosericeum*	Opiliones	Myriopoda	Tipulidae	Homoptera	*Omocestis viridulus*	*Serica brunnea*	*Liodes dubia*	*Loricera pilicornis*	*Lumbricidae*
15	10	—	4	—	34	—	19	7	—	3	—	—	—	—	—	—	13
6	45	—	15	5	186	—	131	4	156	1	—	—	—	—	—	—	13
—	7	—	2	4	139	4	58	—	986	—	—	—	—	—	—	—	1
—	420	—	8	11	76	1	36	—	1988	—	—	730	1	3	6	—	22
—	1517	—	4	20	64	1	58	—	1695	—	—	339	3	—	—	—	40
—	2552	12	21	50	23	1	60	—	207	—	28	61	—	—	—	—	23
1	697	—	8	4	5	—	123	—	5	—	154	5	—	—	—	—	17
—	103	—	4	1	2	—	151	—	—	—	16	2	—	—	—	—	18
2	1	—	2	—	—	—	32	—	—	1	—	—	—	—	—	—	18
3	2	—	3	—	—	—	14	—	—	—	—	—	—	—	—	—	24
3	—	—	7	—	8	—	29	—	—	—	—	—	—	—	—	—	51

TA

Numbers caught in the eleven periods throughout the year o

Month and Dates	Days	Conversion Factor	*Carabus granulatus*	*Nebria brevicollis*	*Notiophilus aquaticus*	*Dyschirius globosus*	*Amara* spp.	*Pterostichus vulgaris*	*Pterostichus strenua*	*Calathus melanocephalus*	*Calathus fuscipes*	*Xantholinus* spp.	*Staphylinus aeneocephalus*	*Tachyporus* spp.
May 29/4 - 18/6	50	1·7	12	1	3	3	20	28	7	—	—	10	6	8
June 18/6 - 18/7	30	1	53	2	3	2	2	15	7	1	—	1	16	29
Jul. 18/7 - 18/8	31	1	14	1	1	—	1	279	—	—	—	1	—	1
Aug. 18/8 - 14/9	27	0·9	16	10	4	4	—	581	—	14	9	38	21	14
Sept. 14/9 - 15/10	31	1	17	14	3	6	—	392	—	57	12	33	36	—
Oct. 15/10- 11/11	27	0·9	—	33	1	4	—	107	—	42	7	3	28	4
Nov. 11/11- 14/12	33	1·1	—	11	2	1	1	13	—	—	1	3	8	—
Dec. 14/12- 14/1	31	1	—	8	3	—	—	7	—	—	—	11	15	1
Jan. Feb 14/1 - 12/3	58	1·9	—	2	1	—	—	2	—	—	—	13	3	—
Mar. 12/3 - 16/4	35	1·2	—	3	3	—	—	1	—	—	—	20	6	—
Apr. 16/4 - 31/5	45	1·5	—	—	9	1	3	2	—	—	—	3	2	—

E 2

e UNGRAZED ground converted to a standard period of thirty days.

Aphodius spp.	*Longitarsus* spp.	*Longitarsus jacobaeae*	*Sitona* spp.	*Apion apricans*	*Myrmica* spp.	*Forficula auricularia*	Araneida (spiders)	*Trombidium holosericeum*	Opiliones	Myriopoda	Tipulidae	Homoptera	*Omocestus viridulus*	*Serica brunnea*	*Liodes dubia*	*Loricera pilicornis*	*Lumbricidae*
1	1	—	16	1	15	—	250	28	2	1	—	—	1	—	—	—	6
1	1	—	1	—	142	—	84	2	150	—	—	—	—	1	—	—	15
—	—	—	1	—	5	—	—	—	3	—	—	—	—	60	—	—	10
—	1	44	—	—	20	2	28	1	1037	—	—	121	8	16	19	2	19
—	14	153	1	3	11	2	19	2	1195	—	7	141	2	—	7	1	35
—	63	100	2	4	22	—	13	—	1167	—	16	30	2	—	—	5	56
—	88	32	1	—	5	—	29	—	164	—	106	12	—	—	—	—	26
—	19	17	—	—	4	2	228	—	62	—	—	7	—	—	—	—	35
—	2	2	—	—	1	—	130	—	5	—	—	1	—	—	—	—	13
1	1	1	—	—	3	—	94	—	3	—	—	—	—	—	—	—	15
2	—	—	1	2	1	—	9	—	2	—	—	—	—	—	—	—	70

former than in the latter. This is confirmed by Boyd (1957 a and b). The earthworm catches from the same traps showed that the dominant species on the ungrazed ground is *Eiseniella tetraedra* a species known mostly from limnic habitats. This earthworm was not found on the grazed ground.

Apart from pure numerical differences there are also differences in the timing of abundance in the two plots. A glance at the histograms (Fig. 1) shows (i) that peaks occur on one plot which do not occur on the other, and (ii) that ostensibly similar peaks in both plots are out of phase by a few weeks. Good examples of unmatched peaks are seen in the cases of the July peak of *Amara* spp., the August one of *Sitona* spp., the August and October ones of *Notiophilus aquaticus* and the July one of *Tachyporus* spp. These peaks may be caused by (a) species having distinct periodicity in the two habitats or (b) more than one species being considered simultaneously, some having distinctly different periodicity than others. This latter point (b) is considered to be less important than the former, but elements of both are probably present in some cases. Of the four cases cited, three have peaks in the grazed plot unmatched by the ungrazed, and one (*Notiophilus*) has unmatched peaks in both the grazed and ungrazed.

Outstanding examples of (ii), similar peaks out of phase, are shown by the August-September peak of *Pterostichus vulgaris*, the July-September one of *Xantholinus* spp., the September-October one of *Longitarsus jacobaeae*, the May-June one of *Sitona* spp. and spiders, the August-October one of Opiliones and the September-October one of the Lumbricidae. Conditions on each plot, however, have a different effect ; of the seven cases cited, four have the peaks more advanced on the ungrazed and three on the grazed plots.

The differences in the community of snails on both sides of the fence are shown in Table 6. The dune is included to show the occurrences of the important dune-*machair* species *Cochlicella acuta*. On this particular transect this species was not found on the *machair* and seemed to disappear from the community as *Ammophila arenaria* disappeared from the sward on the dune-*machair* transition. The outstanding difference between the communities on the grazed and ungrazed ground was the presence of *Oxychilus alliarius* on the ungrazed and its absence from the grazed. On the other hand, *Helicella itala*, *Vitrina pelucida* and the slugs appeared to be more numerous on the grazed ground. *Helicella itala* was the only species of snail caught in the pit-fall traps, and in very small numbers though they were abundant on the ground.

Differences between months

It is intersting to note that though the histograms for the two plots differ greatly in quantity, they are in many instances similar in form, with synchronous peaks. In some the peaks appear to be a month out of phase. This might be caused by the burst of activity of a group occurring only a few days apart in the two plots, one immediately before the clearance of the traps, and one immediately after. Such might well be the case for example in the July-August peaks of *Xantholinus* spp. Others, like the September-October-December ones of *Staphylinus aeneocephalus*, are, however, probably out of phase by a month or more. Those groups which overwinter as larvae will

TABLE 3

Numbers caught in each trap on the GRAZED ground in one year.

Trap	*Carabus granulatus*	*Nebria brevicollis*	*Notiophilus aquaticus*	*Dyschirius globosus*	*Amara* spp.	*Pterostichus vulgaris*	*Pterostichus strenuus*	*Calathus melanocephalus*	*Calathus fuscipes*	*Xanthodinus* spp.	*Staphylinus aeneocephalus*	*Tachyporus* spp.	*Aphodius* spp.	*Longitarsus* spp.	*Longitarsus jacobaeae*	*Sitona* spp.	*Apion apricans*	*Myrmica* spp.	*Forficula auricularia*	Araneida (spiders)	*Trombidium holosericeum*	Opiliones	Myriopoda	Tipulidae	Homoptera	*Omocestus viridulus*	*Serica brunnea*	*Liodes dubia*	*Loricera pilicornis*	Lumbricidae
Trap 1	2	1	—	5	4	8	—	60	4	13	124	109	—	651	1	7	6	67	—	70	—	629	2	36	145	—	1	—	—	21
Trap 2	1	1	5	13	3	12	1	37	4	19	104	68	5	560	1	15	18	44	—	99	1	469	1	31	122	—	—	4	—	39
Trap 3	1	2	1	2	3	6	—	14	3	6	94	30	3	647	2	17	3	37	—	94	2	525	—	19	99	—	2	6	—	46
Trap 4	9	—	—	1	3	16	—	25	1	6	108	56	6	394	—	8	11	56	2	116	—	587	1	29	90	—	1	—	—	47
Trap 5	1	—	1	15	6	9	—	27	1	11	83	53	8	571	—	3	8	36	1	88	—	499	1	12	93	2	—	7	—	30
Trap 6	2	1	—	15	9	8	—	85	5	5	78	75	3	546	2	12	5	43	1	82	—	484	—	24	225	—	—	3	—	33
Trap 7	4	—	2	3	16	10	—	43	5	5	131	85	4	750	1	12	19	142	1	92	5	481	—	19	137	4	—	—	—	31
Trap 8	—	—	4	1	2	4	3	71	3	3	68	63	13	501	1	9	12	62	1	69	8	546	1	34	133	—	1	2	—	35
Trap 9	8	—	4	4	8	9	—	32	5	5	88	73	4	512	3	12	7	73	1	78	—	699	—	7	89	—	4	4	—	14

TABLE 4

Numbers caught in each trap on the UNGRAZED ground in one year.

Trap	*Carabus granulatus*	*Nebria brevicollis*	*Notiophilus aquaticus*	*Dyschirius globosus*	*Amara* spp.	*Pterostichus vulgaris*	*Pterostichus strenuus*	*Calathus melanocephalus*	*Calathus fuscipes*	*Xantholinus* spp.	*Staphylinus aeneocephalus*	*Tachyporus* spp.	*Aphodius* spp.	*Longitarsus* spp.	*Longitarsus jacobaeae*	*Sitona* spp.	*Apion apricans*	Myrmica spp.	*Forficula auricularia*	Araneida (spiders)	*Trombidium holosericeum*	Opiliones	Myriopoda	Tipulidae	Homoptera	*Omocestus viridulus*	*Serica brunnea*	*Liodes dubia*	*Loricera pilicornis*	Lumbricidae
Trap A	8	10	4	1	5	117	3	11	2	27	16	16	1	25	23	2	3	21	2	139	16	420	1	29	47	1	11	4	—	24
Trap B	6	9	1	8	3	118	—	14	3	18	22	7	—	15	14	2	1	32	—	135	4	309	—	12	30	2	9	6	—	37
Trap C	17	7	3	6	1	110	6	8	2	12	19	10	—	31	9	14	3	47	—	138	3	393	—	27	32	1	9	2	—	32
Trap D	19	12	1	—	3	218	1	13	4	14	20	5	2	16	17	4	—	7	2	126	2	471	—	15	36	—	13	2	—	24
Trap E	13	9	2	1	3	144	7	12	2	7	17	4	—	1	12	2	2	45	—	184	4	450	—	5	24	1	2	4	2	37
Trap F	23	10	5	—	5	174	2	11	1	21	11	4	1	14	14	1	1	28	1	144	1	412	—	11	30	1	3	1	2	51
Trap G	12	11	14	2	6	177	9	16	5	19	23	5	1	38	132	—	1	29	—	103	3	327	—	21	35	2	13	3	2	25
Trap H	2	7	6	1	13	103	—	9	4	12	6	—	1	12	24	2	—	13	—	132	5	354	—	13	29	4	8	—	1	32
Trap K	18	11	4	4	1	218	—	17	3	20	14	12	—	42	93	8	—	9	—	141	14	399	—	13	36	—	6	2	1	22

probably have a unimodal annual distribution, and those which do so as imagos or adults a bimodal one with bursts of reproduction in spring and autumn. *Pterostichus vulgaris*, *Calathus melanocephalus* and *C. fuscipes* possess the unimodal characteristic and *Notiophilus aquaticus*, *Xantholinus linearis*, *Sitona* spp., spiders and Lumbricidae, the bimodal.

A glance at the annual variation of monthly means of temperature and rainfall (Table 5) shows the maritime character of the Tiree weather. From June to September 1955 the air temperature was consistently higher than the average for the period 1943-52 and the rainfall in July and August very much lower than average. During this drought the grazed pastures were scorched and the soil dried out to a depth of about 8 cms. on the grazed plot, but the soil surface on the ungrazed plot remained moist. These abnormal conditions almost certainly have emphasised the differences in the two habitats.

The July-August period constitutes a climatic extreme to which one would expect to find a different reaction in the grazed and ungrazed habitats, one being much more insolated than the other. A decline in activity occurs in both plots as the drought advances but the burst of autumn activity commences in the ungrazed plot while the drought is most intense. In the case of the grazed it is co-incidental with September rains. The dry conditions of July and August favoured *Dyschirius globosus*, *Pterostichus vulgaris*, *Xantholinus* spp., *Tachyporus* spp., and Opiliones, most of which were more active on the grazed plot.

TABLE 5

Rainfall and mean temperature data from Tiree.

Month	1955—56		Mean 1943—52	
	F°	mm	F°	mm
May	48·1	50	50·1	52
June	53·3	80	54·0	86
July	56·7	91	58·5	10
August ..	57·1	89	59·3	33
September ..	54·3	134	56·1	163
October ..	51·1	144	49·3	165
November ..	46·1	123	49·4	45
December ..	43·5	145	43·0	160
January ..	41·6	146	40·9	96
February ..	41·5	83	39·3	55
March ..	43·7	75	44·5	36
April	46·3	77	44·7	60

The winter was colder and drier than usual, but was much more normal than the summer had been. The January-February extreme had a similar effect on both plots bringing activity to a minimum. *Xantholinus* spp., *Staphylinus aeneocephalus* and the spiders are all fairly active throughout. *Xantholinus* spp. are unique among all the groups ; this group is more active

during extreme periods of weather than during clement periods. Indeed between November and March while both temperature and rainfall were consistently falling the activity of *Xantholinus* spp., was increasing.

Most specimens obtained in each group were adults. Three notable exceptions are the spiders, Opiliones and Lumbricidae. In the case of the insects all but a few were imagos. The groups can be divided into (i) those which were caught throughout the year in one or both habitats and (ii) those which were not caught throughout the year.

Differences between traps

In Tables 3 and 4 are set forth the catches from the traps over the period of twelve months. In a perfectly uniform habitat over the same sampling period each trap would stand an equal chance of catching the same number of animals. It will be remembered from the description of the habitat that there is a strong suggestion of uniformity. It is, superficially at least, a highly uniform type of terrestrial habitat, and yet when considered from the single view point of animal activity, it is heterogeneous. Ignoring groups with zero values as not giving the necessary scope for variation, there are sixteen on the grazed plot and seventeen on the ungrazed plot to be considered in a test for heterogeneity (Table 7).

The values of χ^2 with 8 degrees of freedom are, at the 0·05 level 15·507 and at the 0·1 level 13·362. On the grazed ground three groups have significant heterogeneity at the 0·05 level and three at 0·1 ; on the ungrazed five groups have significant heterogeneity at 0·05 and two at 0·1. Another seven groups (five on the grazed and two on the ungrazed) have significant heterogeneity at the 0·2 level, but this is not a strong rejection of homgeneity. This heterogeneity can be explained on the basis of the variability in the following :—

(i) sward and soil,
(ii) traps (human ingenuity could not make these identical),
(iii) animal aggregation (breeding clusters),
(iv) trampling and dung of cattle,
(v) predatory activity (*Sorex minutus* and *Sturnus vulgaris*).

The results, however, reveal a measure of both hetero-and homogeneity and probably more of the latter than can be observed in most other local natural systems. The range in values of 2 shows how this variation manifests itself on surface-dwelling forms, and it is highly likely that this reflects a corresponding variation throughout the entire fauna. What in fact has been studied is animal activity in one stratum in two comparatively simple and closely related systems of fairly uniform appearance, the only obvious variable being the composition of the sward.

DISCUSSION

One of the principal techniques in forestry and wildlife management in Britain at present is to change the grazing regime of a locality by the erection of fences which are proof against herbivorous and sometimes predatory mammals. This is a technique which produces desired results in the form of growth of vegetation or the increase in the numbers of animals, and produces them fairly

quickly. The finer consequences of grazing changes as they affect all departments of the ecosystem are very incompletely known, however, and here an attempt has been made in a favourable locality to demonstrate such changes in the status of the soil invertebrates.

Due to the almost absolute effect created by the stock-proof fence on a grassland free from wild herbivores (the effects of the field-mouse and the hare are probably extremely small and can be overlooked), the non-grazing change can be seen to good advantage. Practically all species and other higher taxonomic groups considered have undergone a change in status on the ungrazed ground. What exactly this change is would be difficult, if not impossible, to describe in absolute numbers, but, if pit-fall trap catches can be relied upon to give an index of such, the change is undoubtedly great. It affects large predatory forms such as *Carabus granulatus*, *Pterostichus vulgaris* and *Staphylinus aeneocephalus*, and small herbivorous ones such as *Longitarsus* spp., and *Sitona* spp. It affects fast moving Opiliones and slow moving Mollusca. It affects both hard bodied beetles (Coleoptera) and soft bodied earthworms (Lumbricidae). The overall effect is an interconnected complex of the individual effects.

TABLE 6

Numbers of Mollusca obtained in six 900 sq. cm (1 sq. ft.) quadrats in three stations including the grazed and ungrazed grassland, in October.

SPECIES / STATIONS	*Helicella itala*	*Cochlicella acuta*	*Vitrina pellucida*	*Oxychilus alliarius*	*Cochlicopa lubrica*	*Acanthinula aculeata*	SLUGS
UNGRAZED GRASSLAND (AIRFIELD) ..	1	—	10	25	3	3	4
GRAZED GRASSLAND (MACHAIR) ..	8	—	29	—	—	—	13
NEIGHBOURING DUNE (STABLE) ..	10	44	17	—	2	—	4
NEIGHBOURING DUNE (UNSTABLE) ..	7	59	—	—	—	—	—

The distribution of earthworms in the soil has been compared by Guild (1952) to the distribution of plant species in a sward, and this concept can be suitably adopted here as an aid to the understanding of the distribution of the soil fauna generally. The botanical concept of seral succession (Tansley 1939) applied to this particular situation by Vose, Powell & Spence (1956)

TABLE 7

Analysis of the heterogenity of the monthly counts of numbers caught in taxonomic groups, which did not possess a zero value.

Group	Grazed Ground			Ungrazed Ground		
	Mean	Variance	Variance/ Mean	Mean	Variance	Variance/ Mean
1. *C. vulgaris* ..	—	—	—	13·1	240	18·31
2. *N. brevicollis* ..	—	—	—	9·56	105·75	11·07
3. *N. aquaticus* ..	—	—	—	4·44	38·0	8·55
4. *D. globosus* ..	6·56	84·375	12·87	—	—	—
5. *Amara* spp. ..	6·0	60·5	10·08	4·44	35·5	7·99
6. *P. vulgaris* ..	9·11	105·25	11·55	153·22	2,052·2	13·4
8. *C. melanocephalus* ..	43·78	551·2	12·6	12·33	180·125	14·60
9. *C. fuscipes* ..	3·44	15·875	4·61	2·89	11·0	3·68
10. *Xantholinus* spp. ..	8·11	100·875	12·44	16·67	348·5	20·91
11. *S. aencocephalus* ..	97·55	442·5	4·5	19·33	334·0	17·28
12. *Tachyporus* spp. ..	68·0	485·25	7·1	—	—	—
14. *Longitarsus* spp. ..	570·22	10,583·5	18·6	21·56	179·3	8·3
15. *Longitarsus jacobaeae*	—	—	—	37·56	1,932·8	51·2
16. *Sitona* spp. ..	10·55	143·45	13·59	—	—	—
17. *Apion apricans* ..	9·89	141·625	14·32	—	—	—
18. *Myrmica* spp. ..	62·22	1,070·9	17·2	25·67	211·7	8·2
20. Spiders ..	87·56	222·0	2·5	138·0	447·0	3·2
21. *T. holosericeum* ..	—	—	—	5·8	66·5	11·47
22. Opiliones ..	546·56	6,078	11·1	392·78	2,923·9	7·4
24. Tipulidae ..	23·33	718·125	30·78	16·22	358·0	22·07
25. Homoptera ..	125·89	1,853·9	14·7	33·22	41·7	1·3

can be adopted also. The change found in the soil fauna between grazed and ungrazed *machair* in Tiree can be interpreted as a stage in the Hebridean shell-sand sere described zoologically. *Carabus granulatus, Nebria brevicollis, Pterostichus vulgaris, Longitarsus jacobaeae, Serica brunnea, Liodes dubia, Loricera*

pilicornis, *Lycosa pullata*, *Oxychilus alliarius* and *Eisenella tetraedra* (Boyd 1957*b*), for instance are important zoological components in the rank Festucatum, but are not so on the grazed *machair*. They illustrate zoologically a stage in time in a dynamic system evolving from a grazed maritime grassland to heath. If this were applied generally to all changes of grazing regime, the nature of the sere would vary greatly according to how much change in grazing pressure was achieved, both wild and domesticated stocks included, and of how much interference is caused, particularly in the ungrazed ground, by planting of trees, cutting and burning vegetation, draining, and controlling animals. In small plots " observer " effect is also encountered.

The effect of fencing is unique in each situation. No doubt, however, the situations can be classified as an aid to forecasting changes beyond superficial vegetational and faunistic levels. The class into which the situation just described in Tiree would be placed is not common, but it is nevertheless important because of its comparative simplicity.

SUMMARY

1. A pit-fall trap survey was carried out in Tiree, Argyll to demonstrate the differences in the soil fauna between grazed and ungrazed (twelve years standing) *machair*. An additional quadrat survey was carried out to show differences in communities of snails and slugs (Mollusca).

2. The habitat is a highly uniform type of grassland which has never been tilled. The sward is a *Festuca-Trifolium-Plantago-Lotus-Galium* complex. The soil is about 15 cms. deep and is a vegetable mould shell-sand mix : pH 7·7, $CaCO_3$, content 60 per cent dry weight, loss of weight on ignition 15 per cent dry weight. No rabbits (*Oryctolagus cuniculus*) are present in Tiree. The climate is maritime.

3. The catch of the pit-fall traps consists mainly of arthropods, and is analysed qualitatively. Over eighty species of invertebrate were identified and some of these are grouped together for subsequent quantitative analysis.

4. The numerical differences between catches on grazed and ungrazed plots are great. Taxonomic groups are classified into those which are favoured by the grazed conditions and those by the ungrazed, both in numbers and biomass.

5. The differences in timing of abundance peaks on grazed and ungrazed ground are analysed and classified as those which occur in one plot and not in the other, and ostensibly similar peaks in both plots which are out of phase. The outstanding difference in the mollusc communities is the presence of *Oxychilus alliarius* on the ungrazed ground and its absence from the grazed.

6. The peaks of annual fluctaution of the taxonomic groups are analysed month by month. The ecosystem has a bimodal fluctuation with peaks in early summer and autumn. Most groups have a single major peak in autumn, a few in early summer, and a few in both early summer and autumn. The numbers caught during climatic extremes in mid-summer and mid-winter are discussed. *Xantholinus* spp., is the only group seen to possess peaks during both extremes, a few others were seen to possess peaks at one or other of the extremes, usually the summer one.

7. The pit-fall traps have an equal chance of catching animals in a homogeneous habitat. The catches are heterogeneous in what appears to be a highly uniform type of habitat. Reasons for heterogeneity are discussed.

8. Fencing is at present an important technique in forestry and wildlife management in Britain. The finer consequences are almost unknown. The invertebrate distribution is described in terms of a seral succession, with particular reference to the shell-sand sere in the Hebrides. The case described in Tiree may be important because of its comparative simplicity.

ACKNOWLEDGMENTS

The author is indebted to the following for advice connected with this paper : C. Gordon Blower (Myriopoda), M. V. Brian (Myrmica), Mrs E. M. Belton (Curculionidae), R. A. Crowson (Coleoptera), Mrs E. A. Crowson (Araneida), A. B. Duncan (Tipulidae), W. Russell Hunter (Mollusca), D. K. McE. Kevan (Orthoptera), J. G. Sheals (Acarina), A. R. Waterston (Homoptera) and M. D. Mountford (Statistics). Mr R. A. Crowson and Dr J. D. Lockie kindly read the manuscript and gave helpful criticism. The weather data were supplied by the Meteorological Office in Tiree. The field work was done with the aid of a grant from the Nature Conservancy to the University of Glasgow. The author is also indebted to Professor C. M. Yonge C.B.E., F.R.S., and Dr J. D. Robertson F.R.S.E. for their interest and encouragement.

REFERENCES

Boyd, J. Morton (1957a). The Lumbricidae of a dune-machair soil gradient in Tiree, Argyll *Ann. Mag. nat. Hist.* (12) **10** : 274 - 82.

Boyd, J. Morton (1957b). Comparative aspects of the ecology of Lumbricidae on grazed and ungrazed natural maritime grassland. *Oikos* **8** : 107 - 121.

Boyd, J. Morton (1958). The ecology of earthworms in cattle-grazed machair in Tiree, Argyll. *J. Anim. Ecol.* **27** : 147 - 157.

Gilbert, O. (1956). The natural histories of four species of *Calathus* (Coleoptera, Carabidae) living on sand dunes in Anglesey, North Wales. *Oikos* **7** : 22 - 47.

Guild, J. W. McL., (1952). The Lumbricidae in Upland Areas II. Population variation on hill pastures. *Ann. Mag. nat. Hist.* (12) **5** : 286 - 292.

Kloet, G. S. & Hinks, W. D. (1945). *A check list of British insects.* Stockport.

Manely, G. (1948). The climate of the Hebrides. *New Naturalist, Lond.* 77 - 82.

Tansley, A. G. (1939). *The British Islands and their vegetation.* Cambridge.

Vose, P. B., Powell, H. G. & Spence, J. B. (1957). The machair grazings of Tiree, Inner Hebrides *Trans. bot. Soc. Edinb.* **37** : 89 - 110.

THE EFFECT OF INDUCED HYPOTHYROIDISM ON THE DERMAL MELANOPHORES OF TELEOSTS

BY

P. Y. FORTUNE

Zoology Department, University College of Wales

[Accepted 10th November, 1959]

(With 1 figure in the text)

The melanophores of *Phoxinus phoxinus* and *Salmo gairdnerii* remain expanded during an initial phase in development. Treatment with thiourea prolongs this phase, which is associated with a hypothyroid condition. The young fry show a difference from the adults in their rate of response to environmental changes. It is suggested that this is due to an internal change, arising as a result of metabolic stress and causing an endocrine imbalance. No effect of thiourea on the melanophores of isolated skin strips, or on the adults of *Phoxinus* could be demonstrated.

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INTRODUCTION

Colour change is frequently associated with adaptation to the visual background, but evidence has accumulated to indicate that in teleost fish at least this change cannot always be interpreted as adaptive to such conditions. A relationship between thyroid activity and colour is apparent although its exact nature is uncertain. An increase in pallor with thyroid dosage has been attributed to concentration of the melanin (Robertson, 1949) and to decrease in the amount of pigment (Robertson, 1949 ; La Roche, Leblond & Prefontaine, 1949, 1950). It has also been associated with thickening of the integument (La Roche & Leblond, 1952) and increased guanine deposition (Robertson, 1949 ; Hoar, 1951). Goitrous fish develop excessive black pigment (Marine & Lenhart, 1910). Conversely, thyroidectomy by means of radio-iodine reduces superficial pigmentation (La Roche & Leblond, 1954).

In each case the experimental animals have been members of the Salmonidae and the colour changes consequent on thyroid dosage have been compared with those occurring during metamorphosis from parr to smolt, when the thyroid is hyper-active (Hoar, 1939 ; Landgrebe, 1941 ; Fontaine, 1948 ; Roberston, 1948, 1949). A similar change could be induced in the brown trout which does not normally show a pronounced metamorphosis ; parallel experiments with the

eel proved negative (Landgrebe, 1941). Experiments with excised skin strips (Robertson, 1951) seem to indicate that the melanin-concentrating effect of the thyroid is not solely associated with metamorphic phenomena.

These results suggest that in certain circumstances, in this case variations in thyroid activity, the tint of the fish reflects internal conditions in contrast to the background colour effect. The present work is an attempt to test this assumption by studying the colour of a teleost under conditions of induced thyroid hypoactivity.

MATERIAL AND METHODS

Phoxinus phoxinus was selected as the experimental animal, for it shows no metamorphic type colour change during its life history and is easily kept in the laboratory. Eggs and adults were obtained from Lake Windermere. The fish were kept in groups in two litres of well aerated water. The eggs were hatched out and the fry maintained in shallow aerated water. For comparison, eggs of *Salmo gairdnerii* were hatched out under similar conditions. All animals were fed on dried food.

Immersion in 0·05 per cent thiourea (0·05 gm./100 ml. water) caused marked histological modification of the thyroid in both the fry and adults and was adopted as a suitable method for inducing hypothyroidism. To avoid undue handling of the fry, half the solution was changed every two days. Mortality was low. In the case of the adults the solution was changed twice weekly.

The expansion of the melanophores of the living specimens was estimated using Hogben's melanophore index (M.I.) (Hogben & Gordon, 1930). The number of melanophores was determined by counting those occurring in a unit area at the base of the caudal fin. Counts were made on freshly killed specimens. Specimens were fixed in Bouin's and stained with Masson's trichrome stain for histological examination of the thyroid.

EXPERIMENTAL

A. *Excised skin strips*

Preliminary experiments on excised skin strips of adult *Phoxinus*, following Robertson's method (1951), were carried out to determine whether there was a direct effect of thiourea upon the melanophores.

Strips of skin, approximately 10 mm. × 5 mm. were taken from the lateral abdominal region of large minnows, (a) with expanded melanophores through being kept on a dark illuminated background, (b) with contracted melanophores through the skin strips being immersed in a 0·0005 per cent solution of adrenaline. The strips were placed in 50 ml. of solutions of the following made up in 0·9 per cent NaCl buffered with McIlvaine's citric–phosphate buffer to pH 7·1 and kept at 10°C.

1. control
2. + 0·05 per cent thiourea
3. + extract from 1 gm. dried thyroid preparation which was approximately 2 per cent.

The strips were examined at intervals over a period of six hours and the melanophore index estimated.

The results show that thyroid as well as adrenaline can initiate concentration of melanin (Table 1). In both the control and the thiourea solutions the M.I. reaches an intermediate value between 3 and 4, regardless of whether the melanophores have previously been expanded or contracted. Thiourea does not affect the speed with which this equilibrium is attained so that it would appear to have no direct influence on the melanophores.

TABLE 1

The figures represent the average melanophore index from four skin strips of *Phoxinus* adults. They indicate the dispersion caused by each solution and the time taken to establish an equilibrium.

Sol. / Time	Melanophores previously expanded i.e. taken from dark fish.					Melanophores previously contracted in adrenaline solution.				
	0 hr.	1 hr.	2 hr.	4 hr.	6 hr.	0 hr.	1 hr.	2 hr.	4 hr.	6 hr.
Control	5·0	3·5	3·5	3·5	3·5	1·0	1·0	2·0	4·0	4·0
+Thiourea ..	5·0	3·0	3·5	3·5	3·5	1·0	1·0	2·0	3·5	3·5
+Thyroid Extract	5·0	2·0	1·5	1·0	1·0	1·0	1·0	1·0	1·0	1·0

B. *Immersion experiments*

It was noticed in a preliminary experiment that fry reared in thiourea appeared darker than the controls. Therefore the number and dispersion of the melanophores during development, both normal and in thiourea, were investigated.

(1) *Melanophore numbers. Fry.*

Phoxinus. Eggs were immersed in thiourea for three days prior to hatching (i.e. four to five days after deposition) and so maintained for three months. The temperature varied between 15-20°C (average 17°C) and they were kept under dim, diurnal illumination on a brown background– an approximation to field conditions.

Melanin appeared and was clearly visible macroscopically three days after hatching. Seven days later the fry assumed the normal upright posture and pigment appeared in quantity. The average size of the thiourea-treated fry was temporarily slightly less than the controls ; no difference was apparent in the " melanophore number : body length " ratio. The results are shown in Table 2a.

Salmo. Eggs were placed in thiourea for eleven days prior to hatching. Pigment was well developed at that time and after twenty-two days there were slight indications that the typical pattern was developing. After sixty-two days the barred pattern was well marked in both the controls and those in thiourea, but it was more intense in the thiourea-treated fish. The results are shown in Table 2b.

The values obtained indicate that there is no obvious difference between the number of melanophores developed in the fry in thiourea and the controls. In this respect *Phoxinus* and *Salmo* appear to be alike.

TABLE 2a

Melanophore numbers. Fry.

The figures represent the melanophore counts in unit areas at the base of the caudal fin (average for five fish). In each case there is a rapid increase in melanophore number during the first few days after hatching. The number then becomes relatively stable and increases gradually. The figures for *Salmo* and *Phoxinus* are not directly comparable.

Phoxinus phoxinus

Days	Thiourea	Control
8	7	9
17	19	13·6
27	19·3	15
37	16	19·5
47	17	18·3
57	21	20·3

TABLE 2b

Salmo guirdneri

Days	Thiourea	Control
3	46	99
5	82·5	98·4
9	105·2	129·2
22	120	94
62	118·5	136·5

(ii) *Melanophore numbers. Adults* (*Phoxinus only*).

Animals were kept under conditions known to cause either increase or reduction of melanophores ; that is, (a) dispersion of the melanophores by constant illumination on a black background and (b) contraction of the melanophores by constant illumination on a white background. The temperature was the same for both groups. The results are shown in Table 3. These figures show the expected loss of melanophores on a white illuminated background and the gain on a dark illuminated background. In neither case is the number affected by thiourea treatment.

TABLE 3

Melanophore numbers. *Phoxinus* adult.

The figures represent the number of melanophores in unit area at the base of the caudal fin (average for five fish). The environmental conditions cause a marked change in the number of melanophores present after fourteen days. This is intensified by further exposure to these conditions.

Days	Dark illuminated		White illuminated	
	Thiourea	Control	Thiourea	Control
14	76	74	63·8	64·3
21	77·8	82	57·1	52·5
28	85·8	87	51·3	47·7
60	105	100·7	47·4	31·8

(iii) *Melanin expansion. Fry.*

Phoxinus. The fish used for the investigation into melanophore numbers were also used to determine the melanophore expansion. In addition, some fry were placed in thiourea immediately on hatching.

For these estimations the fry were kept in small, shallow glass containers. Surface area : depth = 16, thus the ratio was sufficiently high to ensure that there was no oxygen lack. One fry was placed in each container and all containers were then placed in an appropriate vessel. This was either a white illuminated tank or a black tank in complete darkness. The containers were surrounded by water to prevent the temperature rising. Each small container could then be placed on the microscope stage, excess water pipetted off to reduce movement of the fry and the M.I. read as rapidly as possible. The container and fry were then discarded for the remainder of that experiment.

TABLE 4

Melanin expansion. *Phoxinus* fry.

The values obtained represent the average melanophore index for five fish. Each square shows the rate of contraction of the melanophores (a) under white illuminated conditions (W.I.) and (b) in complete darkness (D.). Reading vertically the results are shown for fry of increasing age. Reading horizontally compares fry of the same age under different types of thiourea treatment. In each case the figure at the top of the square indicates the M.I. under the standard conditions. When these figures indicate contraction, the adult state is assumed to have been attained.

Days after hatching / Background	Normal fish		Thiourea treatment before hatching		Thiourea treatment after hatching		Time on background
	W.I.	D.	W.I.	D.	W.I.	D.	
3	5		5		5		0
	5	3·2	5	5	5	4·5	1 hr.
	5	4·4	5	4·5	5	5	2 hr.
	5	4·0	5	5	5	5	4 hr.
7	5		5		5		0
	3·6	3·6	4·5	5·0	3·4	4·6	1 hr.
	3·6	4·0	5·0	5·0	4·0	5·0	2 hr.
	4·0	3·6	5·0	5·0	3·0	4·6	4 hr.
	2·3	4·3	5·0	5·0	3·0	3·6	6 hr.
8	4·3		5		5		0
	2·6	3·3	5·0	5·0	3·3	5·0	1 hr.
	1·0	3·6	5·0	5·0	3·6	3·6	2 hr.
	1·0	2·0	4·5	5·0	3·0	3·0	4 hr.
11	1·5		4·0		2·0		0
	1·1	2·6	4·0	4·5	1·6	3·0	1 hr.
	1·2	2·9	5·0	5·0	1·6	3·8	2 hr.
	1·0	2·5	4·5	5·0	1·6	3·0	4 hr.
	1·3	3·0	5·0	5·0	1·5	3·0	6 hr.
	1·3	2·2	4·5	4·5	1·7	2·5	8 hr.
	2·0	3·0	5·0	5·0	2·0	2·7	24 hr.
26	1·5		3·0		1·0		0
	adult		2·5	3·0	adult		1 hr.
	condition		3·0	3·0	condition		2 hr.
			3·0	3·0			4 hr.

When first hatched the melanophores were expanded (M.I.5) and this state continued for one week after hatching but then contraction occurred. Immersion in thiourea prolonged the initial stage ; this was pronounced when thiourea treatment took place before hatching and less marked if immersion took place on hatching. In the first case the colour variation persisted for forty-six days after hatching, when some light coloured fish appeared among the fry treated with thiourea. At the end of three months there were still some fish with melanophores which were permanently slightly expanded : M.I.3 as opposed to the controls M.I.1. There was apparently no adjustment to external conditions of light and background in the fry treated with thiourea. Contraction of the melanin could be caused by immersion in dilute adrenaline. In the controls contraction took place on a white, brightly illuminated background and in complete darkness. The contraction was more intense under white illuminated conditions than in darkness. In the fry up to a week old the concentration under white illuminated conditions is slow and proceeds at approximately the same rate as in darkness. After a week the response becomes more rapid under both conditions but is not maintained for a long period. Even at eleven days, after exposure for twenty-four hours to the concentrating conditions, the melanophores tend to revert to the expanded condition. At twenty-six days the adult condition is attained and the concentration of melanin under the appropriate conditions can be maintained indefinitely. These results are shown in Table 4 and Fig. 1.

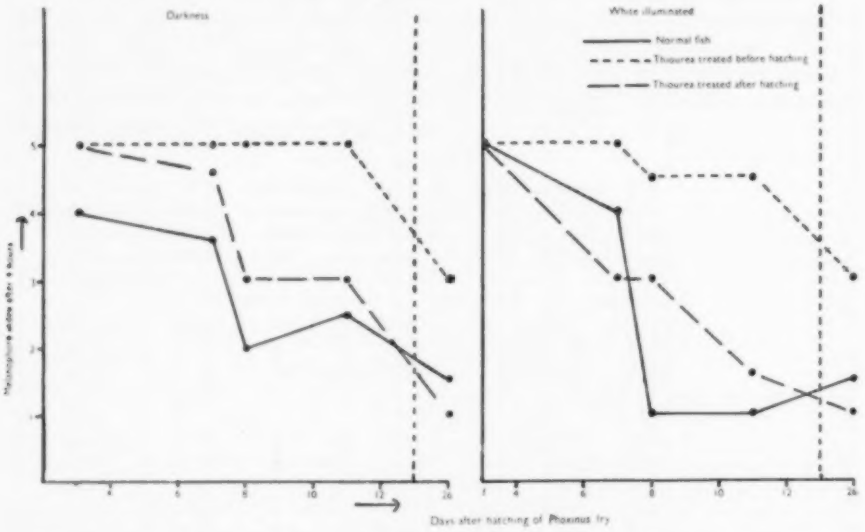

Fig. 1—Melanophore contraction in *Phoxinus* fry of varying ages after 4 hours exposure to concentrating environmental conditions.

Salmo. Similar results were obtained as shown in Table 5.

(iv) *Melanin expansion. Adults (Phoxinus only)*

This was not affected by either short or prolonged thiourea treatment, in every case the normal adaptive change to background and illumination was found.

TABLE 5

Melanin expansion. *Salmo* fry.

Conventions are the same as in Table 4.

Days after hatching / Background	Normal fish		Thiourea treatment before hatching		Time on background
	W.I.	D.	W.I.	D.	
3	5		5		0
	3·0	5·0	5·0	5·0	4 hr.
	3·0	2·5	5·0	5·0	6 hr.
	4·0	3·6	5·0	5·0	24 hr.
5	5		5		0
	4·5	4·1	5·0	5·0	1 hr.
	4·0	4·0	5·0	5·0	2 hr.
	3·6	3·0	5·0	5·0	3 hr.
	3·5	3·1	4·7	4·5	4 hr.
	3·0	2·7	4·5	5·0	5 hr.
	2·7	1·1	4·5	4·5	6 hr.
7	4		5		0
	2·8	1·9	4·3	4·0	16 hr.
	3·3	2·1	5·0	4·2	18 hr.
	2·5	1·3	4·6	4·8	24 hr.
26	1·5		3·0		0
	1·5	1·0	3·0	3·0	1 hr.
	1·5	1·0	2·5	3·0	2 hr.
	1·5	1·0	3·0	2·0	3 hr.
	1·5	1·0	3·0	3·0	5 hr.
	1·0	1·0	2·5	2·0	8 hr.
	1·5	1·0	2·5	3·0	10 hr.
	1·0	1·0	3·0	3·0	24 hr.

C. *Histology of the thyroid gland.*

Phoxinus fry. A thyroid gland with colloid differentiated simultaneously in both the control and experimental animals when the first gill slit was breaking through (thirteen days after deposition at an average temperature of 17°C). After a further two weeks the controls showed few follicles with a low epithelium and abundant green-staining colloid, whilst those treated with thiourea had an increased number of follicles with high epithelium and small amounts of red-staining colloid. Green-staining colloid appeared in the group in thiourea forty-six days after deposition.

Salmo fry. Similar results were obtained.

Phoxinus adult. Control fish showed a low epithelium with either red or green-staining colloid. Thiourea-treated fish showed a greatly heightened epithelium with small amounts of colloid which stained either red or green. The time taken for the maximum effect of thiourea varies with the temperature (Fortune,

1953, 1955). During the prolonged thiourea treatment the temperature was between 17° and 20°C and the maximum histological effect was attained after a fortnight.

DISCUSSION

The use of thiourea for the reduction of the circulating thyroid hormone is, in this case, open to certain criticisms. Firstly there is a possibility of a direct effect of thiourea on the melanophores, but experiments in which excised skin strips were exposed to its influence showed no such effect (Table 1). Secondly thiourea increases the quantity of thyroid-stimulating hormone (TSH) and the melanophores may be responding to this increase rather than to the decrease in the thyroid hormone (TH). As TSH : TH is a self-adjusting ratio, this objection remains valid for any form of thyroid treatment. The melanophores reflect the change of internal conditions due to an alteration in endocrine balance caused by thiourea. It seems probable that the effective change is the reduction of TH in circulation as this hormone exerts an effect on the melanophores of isolated skin strips.

The fry showed development of the red-staining colloid before the green. In those treated with thiourea the red-staining colloid persisted for considerably longer than in the controls, The appearance of some green-staining colloid coincided with the appearance of some light coloured fish (i.e. melanophores contracted) in the experimental group. In the adults small quantities of both types of colloid could be distinguished intra-follicularly and occasionally a few droplets of green-staining colloid appeared intra-cellularly, even after prolonged thiourea treatment. It is assumed that the red-staining colloid, which is normally present in inactive glands, represents the inactive thyroglobulin while the green-staining colloid represents the active thyroalbumin. There seems to be a relationship between the presence of the active thyroalbumin and the onset of the contractile phase of the melanophores.

There have been several reports of the melanophores of teleosts assuming normal functional activity immediately on hatching (see Parker, 1948). In the two species used here there is a tendency for the melanophores of the fry to remain expanded whatever the background, and when contraction does take place it does so slowly. A similar effect has been found in *Fundulus* (Wyman, 1924) where the young larvae in the same environment might show melanophores either expanded or contracted, and the change from one to the other was relatively slow when due to environmental differences. In *Phoxinus* it is interesting to note the variation in rate of response to concentrating conditions in the fry and adults. In the adults the maximum response to W.I. background, when due to hormonal co-ordination, is reached in two hours ; equilibrium in darkness is reached in forty-five hours (Healey, 1951). In the fry the rate of response tends to be the same in both conditions and in one case (W.I.) is slower than in adults and in the other (D) is more rapid. In these fry the contraction can be regarded, not as an adaptive reaction to environment, but as a reflection of changed internal conditions due to a reaction to metabolic stress, caused by a sudden environmental change leading to a readjustment of the endocrine balance. When the new balance becomes

stabilized, the reaction subsides and the melanophores revert to their ' normal ' or expanded condition. Thiourea causes a reduction and even suppression of this metabolic reaction by creating an imbalance due to lack of thyroid hormone and induces a new metabolic level or condition. This interpretation is suported by the fact that adrenaline can override the effect of thiourea. As the fry become older the internal balance becomes more stable and the fry react adaptively to environmental differences in the same way as adults, that is W.I. conditions cause a contraction to M.I. 1·25 and D to 2·1 (Healey, 1951). Some of the fry show an intermediate condition, in that the response to environment appears normal in magnitude but not in timing and it is suggested that in those the stress reaction triggers off the response but stability is achieved more rapidly. The adaptive reaction then takes control and is responsible for the magnitude of the response. In the adult the endocrine balance is more stable; thiourea fails to eliminate the thyroalbumin completely so that the adaptive response due to nervous co-ordination predominates.

The metamorphic type change in the Salmonidae can also be interpreted as a reflection of metabolic stress associated with a readjustment of the endocrine balance. At that point in the life history the endocrine system loses stability, or effects a readjustment to a new stability, as indicated by increased thyroid activity, and the adaptive colour change loses prominence and is overset by the reaction to changed metabolic conditions causing pallor.

ACKNOWLEDGMENTS

I would like to thank Professor E. A. Spaul for his constructive criticism of the work and for his valuable assistance with the manuscript. I would also like to thank Professor C. M. Yonge, in whose department most of the work was carried out, for the generous facilities he has provided.

REFERENCES

Fortune, P. Y. (1953). Thyroid activity in teleosts. *Nature, Lond.* **171** : 483.

Fortune, P. Y. (1955). Comparative studies of the thyroid function in teleosts of tropical and temperate habitats. *J. exp. Biol.* **32** : 504.

Fontaine, M. (1948). Physiologie du saumon. *Ann. Stat. centr. Hydrobiol. appl.* **2** : 153.

Healey, E. G. (1951). The colour change of the minnow (*Phoxinus laevis* Ag.) I. Effects of spinal section between vertebrae 5 and 12 on the responses of the melanophores. *J. exp. Biol.* **28** : 298.

Hoar, W. S. (1939). The thyroid gland of the atlantic salmon. *J. Morph.* **65** : 257.

Hoar, W. S. (1951). Some aspects of the physiology of fish. *Univ. Toronto Biol.* Series No. 59 *Publ. Ont. Fish. Res. Lab.* No. 71 :1.

Hogben, L. T. & Gordon, C. (1930). Studies on the pituitary. VII. The separate identity of the pressor and melanophore principles. *J. exp. Biol.* **7** : 286.

La Roche, G. & Leblond, C. P. (1952). Effect of thyroid preparations and iodide on *Salmonidae*. *Endocrinology* **51** : 545.

La Roche, G. & Leblond, C. P. (1954). Destruction of the thyroid gland of altantic salmon (*Salmo salar* L.) by means of radio-iodine. *Proc. Soc. exp. Biol. Med.* **87** : 273.

La Roche, G. Leblond, C. P. & Prefontaine, G. (1949). Action de l'hormone thyroïdienne. chez le saumon de l'Atlantique (*Salmo salar*) stade ' parr '. *Ann. ACFAS* **15** : 84.

La Roche, G., Leblond, C. P. & Prefontaine, G (1950). Effets de l'hormone thyroïdienne sur le saumon de l'Atlantique : stade parr. *Rev. Canad. Biol.* **9** : 101.

LANDGREBE, F. W. (1941). The role of the pituitary and the thyroid in the development of teleosts. *J. exp. Biol.* **18** : 162.

MARINE, D. & LENHART, L. H. (1910). Observations and experiments on the so-called thyroid carcinoma of brook trout (*Salvelinus fontinalis*). *J. exp. Med.* **12** : 311.

PARKER, G. H. (1948). *Animal colour changes and their neurohumours.* London & New York : Cambridge Univ. Press.

ROBERTSON, O. H. (1948). The occurrence of increased activity of the thyroid gland in rainbow trout at the time of transformation from parr to silvery smolt. *Physiol. Zool.* **21** : 282.

ROBERTSON, O. H. (1949). Production of the silvery smolt stage in rainbow trout by intramuscular injection of mammalian thyroid extract and thyrotropic hormone. *J. exp. Zool.* **110** : 337.

ROBERTSON, O. H. (1951). Factors influencing the state of dispersion of the dermal melanophores in rainbow trout. *Physiol. Zool.* **24** : 309.

WYMAN, L. C. (1924). The reactions of the melanophores of embryonic and larval *Fundulus* to certain chemical substances. *J. exp. Zool.* **40** : 161.

SIX NEW SPECIES OF *MICRATHENA* (ARANEAE, ARGIOPIDAE) FROM SOUTH AMERICA WITH NOTES ON KNOWN SPECIES

BY

ARTHUR M. CHICKERING

Albion College, Albion, Michigan

[Communicated by Dr G. Owen Evans — Accepted 9th February 1960]

(With 90 figures in the text)

Six new species of *Micrathena* are described and figured. These are all selected from unassorted collections loaned by the Department of Zoology, British Museum (Natural History) and Oxford University Museum. The types will be deposited in the appropriate institutions.

In order to further our understanding of the genus additional notes and figures on sixteen species, previously known but inadequately described, are given.

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INTRODUCTION

Early in my acquaintance with the spider fauna of Panama I became strongly impressed by the numerous beautiful specimens of the genus *Micrathena* Sundevall 1833 which very frequently appeared in my collections. On each of my repeated field trips of this region I have tried to add materially to my accumulation of these spectacular animals with the hope of being able to complete an intensive study of the genus in Central America. This task is likely to be completed within the foreseeable future.

With the privilege of working in the British Museum (Natural History) during the summer of 1958 also came an opportunity to study the large number of specimens of *Micrathena* in that institution collected from South America and thus of enlarging my understanding of the whole genus with its many complexities. Additional specimens were also found in collections loaned me for study by staff members of the Oxford University Museum where some of the original collections made by the two Pickard-Cambridges have been deposited. This study was carried out in England as completely as my limited time would permit and has been continued at Albion College and at the Museum of Comparative Zoology at Harvard College.

In the description of new species in this paper I am using a formula somewhat abbreviated from my usual form. No attempt is made to give complete bibliographic references ; only those considered most important are listed. The types of new species have been deposited in the British Museum (Natural History) or in the Oxford University Museum depending upon the source of the loan from which the types have been selected.

As a result of the studies conducted on the genus *Micrathena* I am convinced that the whole group should be carefully restudied and reappraised, perhaps following an extensive period of field work with the express purpose of carefully and systematically collecting the genus all over South America. Members of the genus are exceedingly attractive by reason of their rich and varied colorations, their great variety of anatomical features, and especially the high degree of sexual dimorphism exhibited within the group. I am convinced that confusions have arisen and still exist respecting many species as they are now known. Some of the species described many years ago were inadequately defined and cannot now be determined with certainty. Males are still very poorly known and can only be matched correctly with the corresponding females in a comparatively few instances. Females of certain species have been confused with those of other species and, probably, in some cases the females now regarded as belonging to different species should be united to one. I believe that I have noted several interesting instances of considerable intraspecific variation in respect to spination, coloration, general form, and even the appearance of the rather obscure epigyna upon which we now depend to a great extent for the determination of species. The genus has evolved in a remarkable manner throughout almost the whole of the Western Hemisphere and in a more or less explosive fashion in Central and South America.

GENUS *MICRATHENA* Sundevall 1833

The genus is here accepted essentially as defined by Reimoser so far as females are concerned. He almost completely neglected males. In my judgment, these should now be included in the generic definition but considerable comparative study will be necessary in order to do it. Reimoser (1917) included in his treatment eight species known only from males, eight species for which both sexes were known, and eighty-eight species known only from females. Roewer (1942) listed a total of one hundred and twenty-nine species distributed as follows : Nine species known only from males, twelve known from both sexes, and the remaining one hundred and eight known only from females. Numerous changes in this list will occur with the publication of the series of papers now under preparation and some will be noted in the present publication.

MICRATHENA ACUTOSPINA (Keyserling), 1863

Figs. 1-3

Acrosoma acutospinum Keyserling, 1863 ; Keyserling, 1892. *Micrathena acutospina*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

The author of this species gave only one figure to show the general appearance of the dorsal surface of the female. Reimoser (1917) gave no figures and took his description directly from the original. There are now five specimens in the Keyserling collection in the British Museum (Natural History). One of these has been selected as the lectotype and is here designated as such. The total length of the lectotype is 6·89 mm. (Keyserling gave 11 mm. as the length but no available specimen has nearly that size). Lectotype : Sternum only moderately convex ; with seven tubercles fairly well developed. The abdomen has two long, slender spines reaching from the anterior border forward over the

carapace nearly to lateral eyes ; two lateral spines on each side as represented by the author of the species but the anterior one appears to be variable and in the lectotype is hardly more than a spinule ; the posterior border is widely bifurcate and each fork is divided in a horizontal plane into two spines the

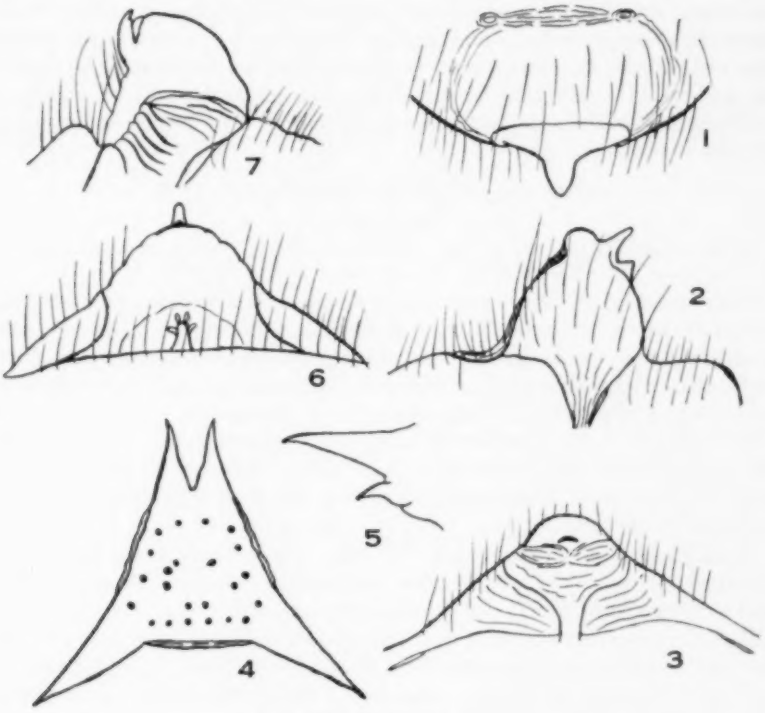


Fig. 1-3, *M. acutospina*
1-3. Epigynum, from below, right lateral view, and posterior view, respectively.
Figs. 4-7, *M. bicolor*
4. Dorsal view of abdomen. 5. Postero-lateral margin of abdomen with third spine. 6-7. Epigynum, posterior view, and right lateral view, respectively.

lower of which is less than half as large as the upper. In order to aid further in understanding of the species I am including three figures of the epigynum (Figs. 1-3). Apparently the species is definitely known only from Columbia and the male remains unknown.

MICRATHENA BICOLOR (Keyserling), 1863

(Figs. 4-7)

Acrosoma bicolor Keyserling, 1863 ; Keyserling, 1892. *Micrathena bicolor*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

Keyserling (1892) published a good description of this species but again gave only one figure, a dorsal view of the whole body. Reimoser (1917) gave

no figures and drew his description from the original publication. Keyserling stated that he had two females from Columbia. I have indentified four others which had been formerly pinned, dried, and later returned to alcohol. These are now in fair condition for study. All specimens are from Columbia. The most important distinguishing features appear to be the following : Length from base of chelicerae to posterior end of postero-lateral spines about 6·7 mm. ; abdominal spines essentially as shown in Figs. 4 and 5 ; small lower posterior spines not visible from dorsal view ; epigynal features shown in Figs. 6 and 7 ; head not raised above thorax, glabrous ; central thoracic fovea hardly discernible and others lacking ; sternum quite convex, with low tubercles as usual. The male is still unknown.

MICRATHENA BIFISSA (Keyserling), 1892
(Figs. 8-11)

Acrosoma bifissum Keyserling, 1892. *Micrathena bifissa*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

Unfortunately, there are now only two immature females in the " type " vial in the British Museum (Natural History). Contrary to his usual practice the author of this species gave an exceedingly brief description accompanied by two figures. A specimen in the Ehrhardt collection appears to belong to this species and agrees well with Reimoser's (1917) treatment. Another specimen in the Museum of Comparative Zoology also belongs here. It seems worth while to add a few important facts concerning what appear to be the most significant features of the species taken from the Ehrhardt specimen which is designated as the hypotype.

Female hypotype. Total length 7·15 mm. Viewed from above, anterior row of eyes strongly recurved, posterior row moderately recurved. Height of clypeus equal to about three fourths of the diameter of AME.

Cephalothorax and *appendages.* Appendages normal to the genus, without noteworthy features. Carapace with a well defined central fovea behind which is a moderately high gibbosity ; also with a fairly well defined pair of foveae in the cephalothoracic groove. Sternum only slightly convex.

Abdomen. Slightly convex dorsally ; deeply and broadly cleft in the middle of the posterior border ; with a total of nine pairs of spines but some are hardly more than tubercles and, very likely, will be found to be somewhat variable in number when a sufficiently large number of specimens is studied (Fig. 8). The epigynum is similar to that of several other species ; its more or less charcteristic features are shown in Figs. 9-11.

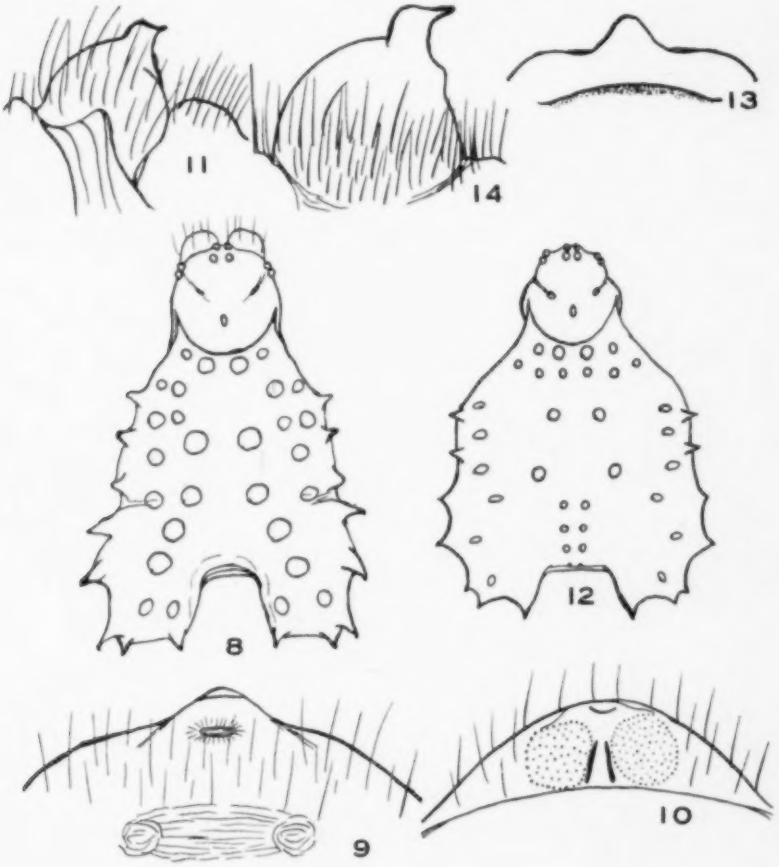
The species appears to be closely related to *M. triserrata* F. Cambridge, *M. brevispina* (Keyserling), *M. quadriserrata* F. Cambridge and some others.

Collection records : All records are from Brazil, including the one in the Museum of Comparative Zoology. The hypotype is from St. Catherine, Humboldt, Joinville, October, 1916. The male is still unknown.

MICRATHENA BREVISPINA (Keyserling), 1863
(Figs. 12-14)

Acrosoma brevispinum Keyserling, 1863 ; Keyserling, 1892. *Micrathena brevispina*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

Keyserling's description is quite adequate but only one figure was given. Apparently the author had several specimens before him but only one seemed to be available during my period of work in the British Museum (Natural History). The general features of this single individual may be stated as follows : Total length 6·44 mm. ; general shape, spines, etc. shown in Fig. 12.



Figs. 8-11, *M. bifissa*

8. Dorsal view of body. 9-11. Epigynum, from below, posterior view, and right lateral view, respectively.

Figs. 12-14, *M. brevispina*

12. Dorsal view of body. 13-14. Epigynum, from below, and right lateral view, respectively.

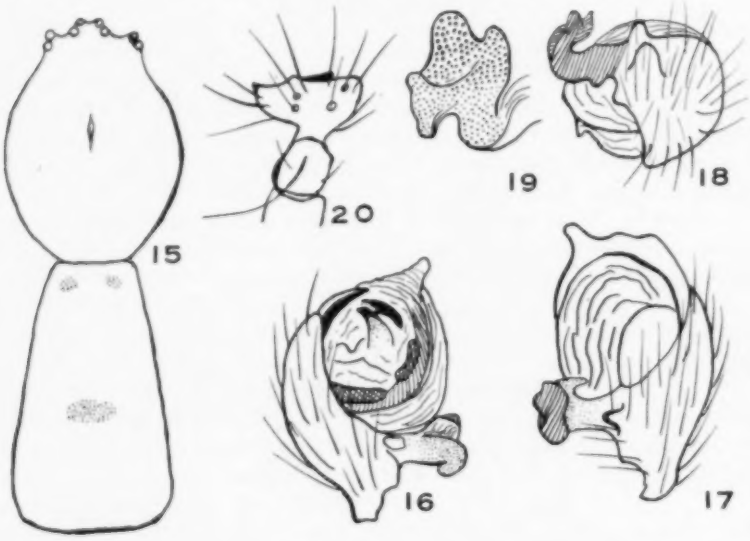
The carapace shows a definite central fovea and a pair of dorso-lateral foveae in the cephalothoracic groove ; somewhat raised behind the central fovea and then descends steeply to posterior border. Sternum quite regularly convex ;

anterior sternal tubercles prominent but others not clearly developed. Colour pattern as indicated by the author of the species but probably, as in other instances, quite variable. Features of the epigynum as shown in Figs. 13 and 14. The single specimen available for study was from Columbia, the only reported habitat for the species. The male is unknown.

MICRATHENA BROWNINGI sp. n.

(Figs. 15-20)

A male *Micrathena* from British Guiana, formerly filed in the collection of the British Museum (Natural History) as *M. vitiosa* (O. P. Cambridge) is quite clearly very different from that species and, in my judgment, must be regarded as new to science. It is, accordingly, herewith described as follows :



Figs. 15-20, *M. browningi* sp. n.

15. Outline of body, dorsal view. 16. Left palpal tarsus ; apophyses and tarsal hook. 17. Ibid.; especially tarsal hook. 18. Ibid.; proximal end of papal tarsus ; especially the tarsal hook. 19. Distal end of palpal tarsal hook ; more enlarged. 20. Palpal tibia and patella ; dorsal view.

Male holotype. Total length 4·55 mm. Carapace 2·15 mm. long ; 1·39 mm. wide opposite interval between second and third coxae where it is widest. General form as shown in Fig. 15 ; considerably flattened. Height of clypeus equal to nearly four times the diameter of AME.

Cephalothorax and *appendages.* Head somewhat lower than thoracic part. Carapace generally smooth, with very slight depressions where marked pits frequently occur in certain species. Viewed from in front, anterior row of eyes very slightly recurved ; central ocular quadrangle wider behind than in front in ratio of 13 : 10. Legs of normal length. Femora without such modified

spines as those in *M. vitiosa*. Other leg spines normal. Without hook on first coxa and without ridge and groove of second femur. Sternum finely granular, moderately convex, with posterior end slightly tubercular. Palp : Tarsal hook totally unlike any other seen by this author ; palpal features as in Figs. 16-20.

Abdomen. General form as shown in Fig. 15 ; possibly two pairs of suppressed spines at postero-lateral angles (not shown in Fig. 15).

Colour in alcohol. Carapace a rich mahog any brown ; sternum a variable yellowish brown ; legs reddish brown with third and fourth somewhat lighter than first and second. Abdomen : dorsum generally black or very dark brown with three whitish spots, indicated in Fig. 15 by stippled areas.

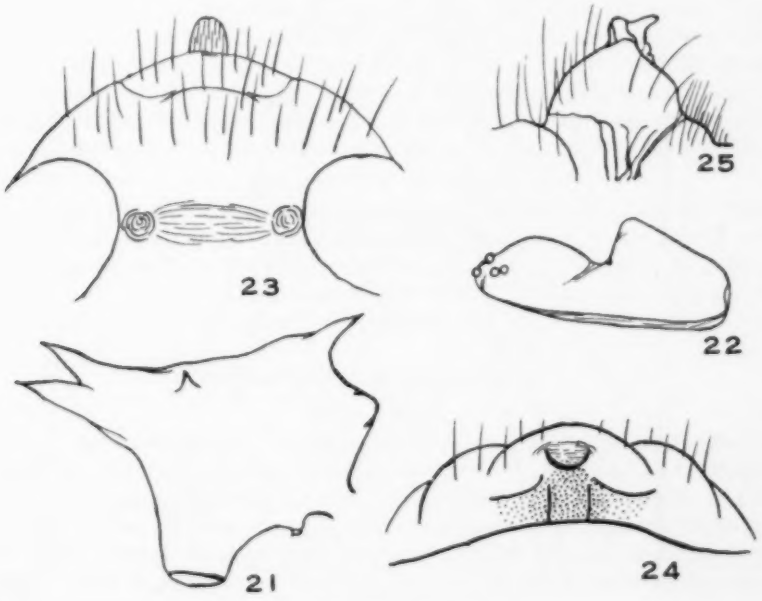
Type locality. Male holotype from British Guiana, St. Diamond, January 5, 1946 (H. C. James, collector). Female unknown. No paratypes.

Holotype. Brit. Mus. (Nat. Hist.). 1949. 12.12.3.

MICRATHENA CRASSA (Keyserling), 1863
(Figs. 21-25)

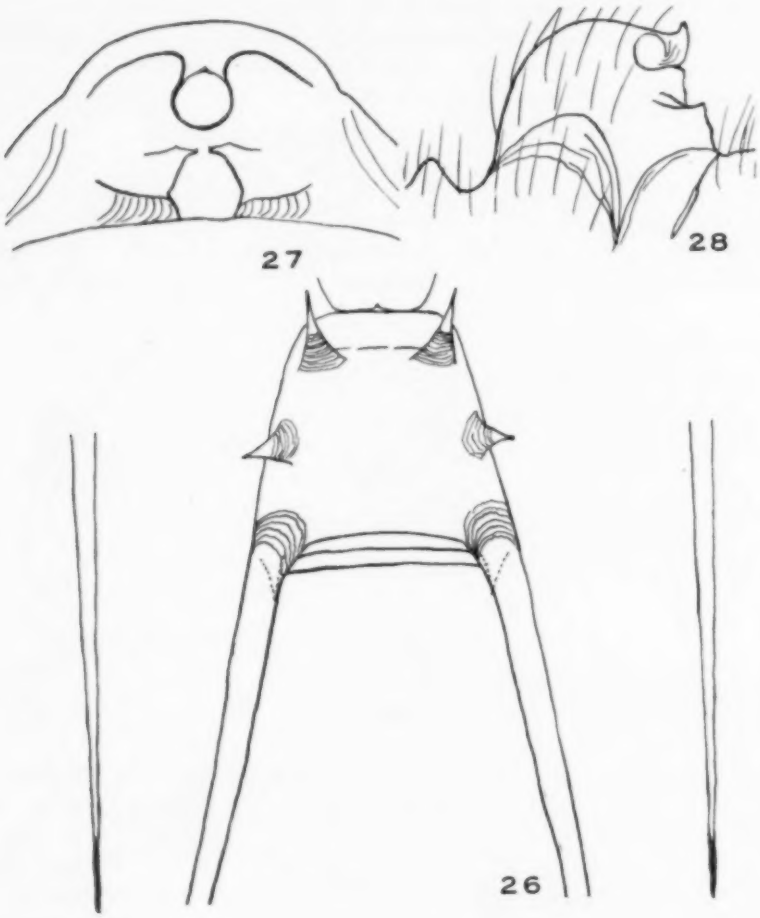
Acrosoma crassum, Keyserling, 1863 ; Keyserling, 1892. *Micrathena crassa*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Petrunkevitch, 1925 ; Roewer, 1942 ; Bonnet, 1957.

Keyserling stated in 1892 that he had six specimens for study. A lectotype should be selected from these. There are now numerous specimens in the



Figs. 21-25, *M. crassa*
21. Abdomen from right side. 22. Cephalothorax, left lateral view. 23-25. Epigynum, from below, posterior view, and right lateral view, respectively.

collection and there is one in the Museum of Comparative Zoology at Harvard College. The most important features for identification of the species appear to be the following : total length from AME to middle of posterior border of abdomen 6·89 mm. ; to posterior end of posterior spines 7·67 mm. (the M. C. Z. specimen is somewhat larger). Head and thorax are well separated by a well defined groove ; the median thoracic fovea is clear and definite ; behind the fovea the carapace is sharply raised (Fig. 22) ; with no dorso-lateral foveae. Sternum moderately convex, with seven tubercles quite well developed. Abdomen : with epigynal features essentially as shown in Figs. 23-25 ; with a



Figs. 26-28, *M. cyanospina*
26. Outline of abdomen, dorsal view (posterior spines offset). 27-28. Epigynum from posterior view and right lateral view, respectively.

pair of rounded anterior tubercles at lateral corners instead of definite spines ; behind these is a pair of marginal spines, quite long and sharply pointed ; then a pair of small marginal spines ; the abdomen is bifurcated posteriorly and each fork is subdivided by a horizontal cleft into two spines the lower of which is slightly longer than the upper. Collection records seem to be restricted to Columbia and Panama as indicated by Keyserling, Reimoser, and Petrunkevitch. The male is still unknown.

MICRATHENA CYANOSPINA (Lucas), 1835

(Figs. 26-28)

Epeira cyanospina, Lucas, 1835. *Plectana cyanospina*, Walckenaer, 1841. *Micrathena cyanospina*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

Reimoser (1917) took his description entirely from the work of Lucas and Walckenaer. He gave no figures of the species. One female was found in good condition in the British Museum (Natural History) from which the following facts are taken : Total length from AME to posterior border of abdomen about 12 mm. ; from AME to tips of long posterior spines about 36 mm. Carapace smooth ; moderately depressed between head and thorax. Sternum moderately convex, rugulose, with three pairs of tubercles well developed and with posterior end tubercular and extended between fourth coxae. Legs with many setigerous tubercles. Abdomen with eight spines as shown in Fig. 26 ; with the long posterior spines greatly extended, being somewhat more than four times as long as the width of the abdomen between their bases. From dried specimens in the British Museum (Natural History) it would be deduced that these extended spines may, in the living animal, lie nearly parallel, diverge from one another, or converge toward each other depending upon the degree of tension within the abdomen (eggs and their degree of development, etc.). The epigynum appears to be distinctive as shown in Figs. 27, 28. The extended spines are a dark brown with a beautiful greenish sheen.

Hypotype female. Apparently collected on October 18, 1922 in British Guiana, Potaro Landing, Potaro River by A. A. Abrahams. There is a badly damaged specimen from Para, Brazil in the Museum of Comparative Zoölogy. The species is only known from Brazil and British Guiana. The male is unknown ; its discovery is awaited with interest.

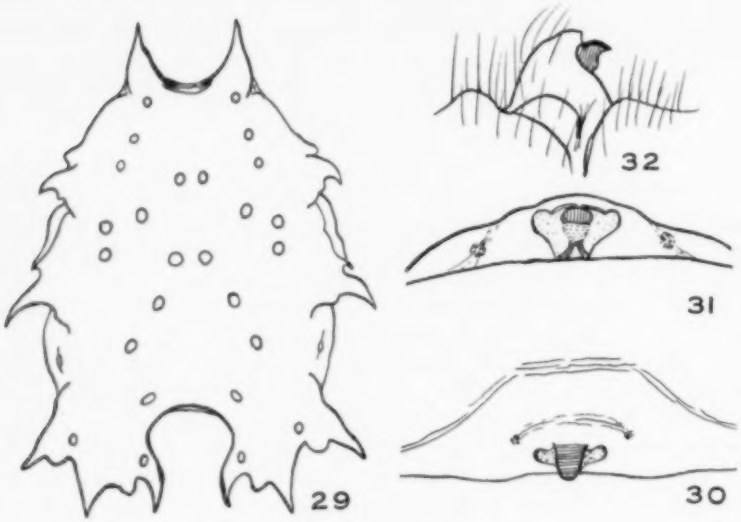
MICRATHENA DECORATA sp. n.

(Figs. 29-32)

Among the specimens of *Micrathena* studied in the British Museum (Natural History) are three females from Columbia which are a part of a large collection deposited in that institution by Dr George Marx after the death of Graf Keyserling. Two of these were, apparently, regarded as representing a new species. Keyserling's description was never published and, perhaps, never prepared. It now seems desirable, therefore, to have these definitely on record as another member of this remarkable genus.

Female holotype. Total length from base of chelicerae to tip of posterior spines 13·33 mm. Carapace 4·55 mm. long ; 3·25 mm. wide opposite interval

between second and third coxae where it is widest. Abdomen 8·19 mm. long from anterior border between anterior spines to posterior border between posterior spines ; 6·60 mm. wide just anterior to bases of posterior spines.



Figs. 29-32, *M. decorata* sp. n.
29. Outline of abdomen, dorsal view. 30-32. Epigynum, from below, posterior view, and right lateral view, respectively.

Cephalothorax and *appendages*. Margin of carapace with numerous setigerous tubercles. Central thoracic fovea distinct, with a moderately well developed gibbosity just posterior to it ; with two pairs of dorsolateral foveae. Sternum moderately convex and somewhat rugulose ; with weakly developed tubercles opposite first, second and third coxae and at posterior end. Legs normal to genus with femora bearing many setigerous tubercles.

Abdomen. General form as shown in Fig. 29. A pair of anterior marginal spines extend over the carapace and are slightly convergent ; with two pairs of short lateral marginal spines each with secondary spines or tubercles at its base. The posterior end is bifurcate with each fork subdivided into three short sharp spines ; the two outer spines on each side with a rounded tubercle. On each side of the chitinous cone surrounding the spinnerets there is a well developed tubercle.

Colour in alcohol. Carapace reddish brown with a yellowish border. Legs reddish brown ; lighter below. Sternum dark brown. Abdomen : Dorsum yellowish white with a bright and shining ornate pattern like a variegated enamelled surface unlike that seen by the author in any other species. Anterior spines variegated, all others dark mahogany brown.

Type locality. Female holotype and two female paratypes from Columbia. The only date given is that on which the collection was received in the British Museum (Natural History), July 1, 1890. The male is unknown.

Holotype. Brit. Mus. (Nat. Hist.). 1890 7.1.6297 ; Paratype. Brit. Mus. (Nat. Hist.) 1890. 7.1.6298.

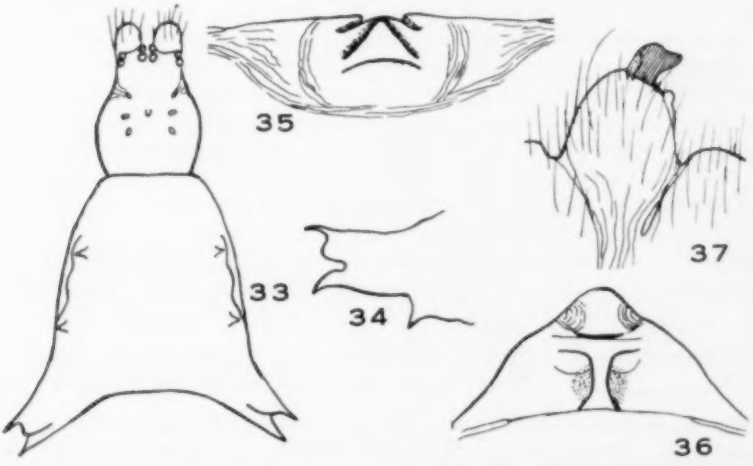
MICRATHENA DIGITATA (C. L. Koch), 1839

(Figs. 33-37)

Acrosoma digitatum C. L. Koch, 1839 ; C. L. Koch, 1851. *Micrathena digitata*, Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

This appears to be another of the lesser known species of the genus. There is a female in the Keyserling collection in the British Museum (Natural History) from Columbia but it is not in good condition. A single female in the Oxford collection is used for the following descriptive material.

Female hypotype. General form, spines, etc. essentially as shown in Figs. 33, 34 ; with no anterior marginal spines ; with two pairs of small dorsal marginal spines ; the posterior end is bifurcated with each fork divided into two spines the more dorsal of which has a large ventral swelling at its base ; beneath each fork there is a small spine, thus completing the set of ten spines. Total length about 7·15 mm. from base of chelicerae to tips of posterior spines. The head is not raised but the thorax is moderately gibbous behind the well defined central fovea ; there are also three pairs of dorso-lateral foveae. The sternum is only moderately convex and has moderately developed lateral tubercles. Fang groove with four promarginal and three retromarginal teeth. The anterior two pairs of tibiae are provided with well defined paired spines on the ventral surfaces ; anterior pair of femora with a series of short stout spines in proximal half ; fourth femora with a series of dorsal spines. The features of



Figs. 33-37, *M. digitata*

33. Outline of body, dorsal view. 34. Right lateral view of posterior end of abdomen. 35-37. Epigynum ; from below, posterior view, and right lateral view, respectively.

the epigynum (Figs. 35-37) are important in identification but as usual in the genus they are obscure here.

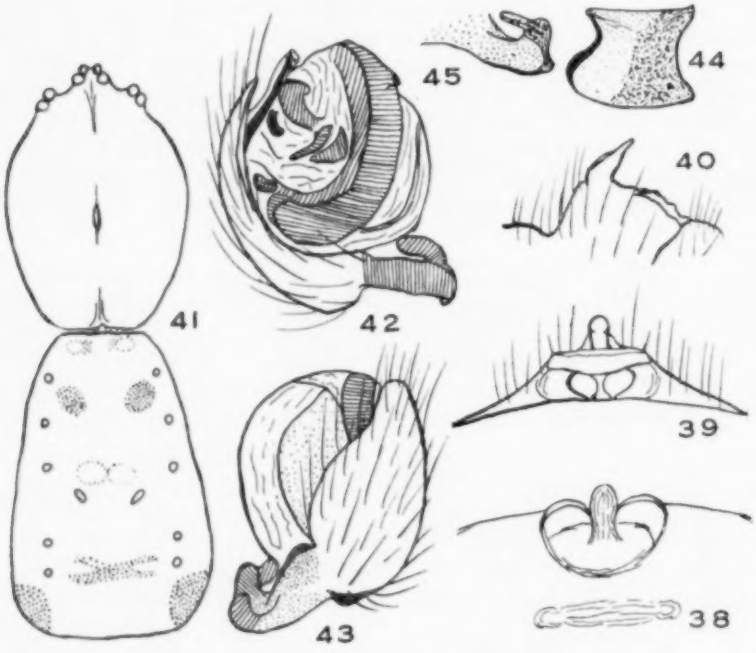
Female hypotype. Found in a part of a collection made by F. O. Pickard-Cambridge and E. E. Austen on a trip up the Amazon from Para to Manaos, January to March, 1896 under the auspices of Messrs. Siemans and Co. in the S. S. Faraday. The male is unknown.

MICRATHENA ELONGATA (Keyserling), 1863

(Figs. 38-40)

Acrosoma elongatum, Keyserling, 1863 ; Keyserling, 1892. *Micrathena elongata*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

So far as I have been able to determine, no figures of the epigynum have been published for this species. It has been thought worth while to include here figures (Figs. 38-40) of this organ to help in identification of the species ; the figures are taken from what might well be selected as the lectotype. In 1892 Keyserling stated that he had a female and a male in his collection. Several examples are now available for study. These include males but they are all



Figs. 38-40, *M. elongata*
38-40. Epigynum, from below, posterior view, and right lateral view, respectively.
Figs. 41-45, *M. evansi* sp. n.
41. Outline of body, dorsal view. 42-43. Two different views of left palpal tarsus. 44 Distal end of palpal tarsal hook, more enlarged. 45. Another view of palpal tarsal hook.

immature and unsuitable for description. Bonnet (1957) has synonomized *M. cala* Chamberlin, 1916 with this species. I have examined this single female specimen and have found it to be immature. Moreover, the abdominal spines seem to indicate that it is not *M. elongata* (Keyserling), hence it will be continued as a valid species.

Female hypotype. Total length from AME to posterior end of short posterior spines 8·78 mm. The median thoracic fovea is distinct ; there are two pairs of moderately well developed dorso-lateral foveae nearly opposite the median fovea. The carapace is rather strongly gibbous just behind the median fovea. The seven sternal tubercles mentioned by Keyserling are moderately well developed. The abdomen bears four pairs of short spines with none on the anterior border ; a pair about one fourth the length of the abdomen from the base, then three on each postero-lateral corner. Immature males, interestingly enough, have an additional pair of spines about half way between the first pair and the posterior end. A male near the final moult indicates that this may be another species in which the male retains well developed spines in the adult state as do males of *M. swainsoni* and a few others. Some of the females in the collection are quite constricted in the posterior third of the abdomen thus producing what has been called a " caudal " extension. The species is definitely known only from Columbia.

MICRATHENA EVANSI sp. n.

(Figs. 41-45)

Male holotype. Total length 3·31 mm. Carapace 1·6 mm. long, 1·07 mm. wide opposite second coxae where it is widest. General form as shown in Fig. 41 ; considerably flattened dorso-ventrally.

Cephalothorax and *appendages.* Carapace smooth with central fovea a rather poorly defined longitudinal groove ; small setigerous tubercles extend around lateral margin. Clypeus receding and little more than twice as high as the diameter of AME. Central ocular quadrangle wider behind than in front in ratio of about 11 : 8. Both rows of eyes procurved when viewed from in front. Legs of normal length. Femora one and two with several long slender spines near distal ends ; tibiae 1 and 2 also with several long slender spines but neither with highly modified spines such as those in M. vitiosa and some others. The hook on the first coxa and the corresponding ridge and groove on the second femur appear to be completely lacking in this species. Sternum moderately convex and with a low posterior tubercle. Palp quite distinctive as shown in Figs. 42-45.

Abdomen. With general form as shown in Fig. 41. Suppressed spines hardly visible at postero-lateral corners.

Colour in alcohol. Carapace a rich mahogany brown, lighter in median area to posterior declivity ; sternum yellowish and variegated ; legs reddish brown above, lighter below. Abdomen : whitish-yellow dorsally ; with a divided central white spot and several poorly defined black spots indicated by stippled areas in Fig. 41.

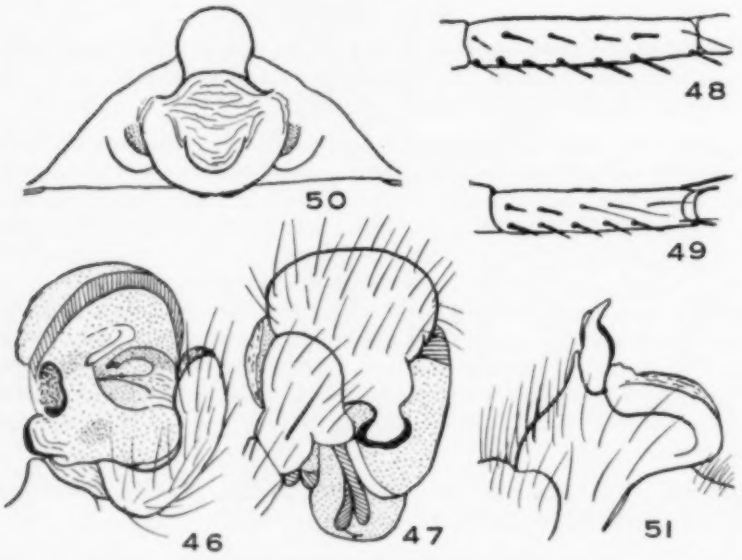
Type locality. Male holotype from Forest Santarem, Brazil ; F. O. Pickard-Cambridge, collector. Only date available is accession date, Sept. 20, 1897. One paratype male from the same locality. These specimens were found with a female *M. duodecimspinosa* (O. P.-Cambridge) but they cannot be males of that species according to our present view.

Holotype. Brit. Mus. (Nat. Hist.). 1897. 9.20.261 ; Paratype. Brit. Mus. (Nat. Hist.) 1897.9.20. 262

MICRATHENA FURVA (Keyserling), 1892
(Figs. 46-49)

Acrosoma furva, Keyserling, 1892. *Micrathena furva*, Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

Only the holotype is now in the British Museum (Natural History) so far as I have been able to determine. The specimen is in good condition except that the left palp has been lost. Since details of the palp are now considered of prime importance I have included figures of this structure to supplement the small figures published by the author of the species. Reimoser only listed this species among the males known at that time (1917). The hook on the first coxa and the corresponding ridge and groove on the second femur are only slightly developed. First and second ventral tibial spines as shown in Figs. 48 and 49. Palpal tarsal features as shown in Figs. 46 and 47. The holotype is from Rio Grande do Sul, Brazil.



Figs. 46-49, *M. furva*
46. Palpal tarsus, right. 47. Right palpal tibia and base of cymbium. 48-49. Right first and second tibiae, respectively, to show ventral spines.
Figs. 50-51, *M. guerini*
50-51. Posterior and right lateral view of epigynum, respectively.

MICRATHENA GUERINI (Keyserling), 1863

(Figs. 50-51)

Acrosoma guerini, Keyserling, 1863 ; Keyserling, 1892. *Micrathena guerini*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

An examination of the two specimens now in the British Museum (Natural History) shows that the epigynum is more complicated than usual in this genus. Apparently, one of the specimens has had the scape broken off and this gives an entirely different appearance to this organ than when it is intact. It is strongly suspected that the scape was broken in the specimen studied by Reimoser (see his Fig. 21, 1917). Two figures of this organ are taken from the specimen in which the scape is intact (Figs. 50, 51) to show some details of the structure.

The most important features of the species as now known appear to be as follows : Total length from AME to posterior border of abdomen between posterior spines 7·8 mm. ; to posterior ends of these spines 9·1 mm. The central thoracic fovea is circular and clearly evident ; the carapace is strongly gibbous just behind the central fovea ; there are two pairs of weakly developed dorso-lateral foveae opposite the central one. The sternum is weakly convex and without well developed tubercles except for a moderately developed pair opposite the first coxae. The abdomen has two pairs of spines, both at the posterior end as figured by Reimoser (1917) ; there are only tubercles at the antero-lateral corners where spines often occur ; in front of the dorsal posterior spines are two pairs of lateral tubercles probably representing small suppressed spines. Known only from Columbia. The male still remains unknown.

MICRATHENA HENSELI Reimoser, 1917

(Figs. 52-57)

M. henseli, Roewer, 1942 ; Bonnet, 1957.

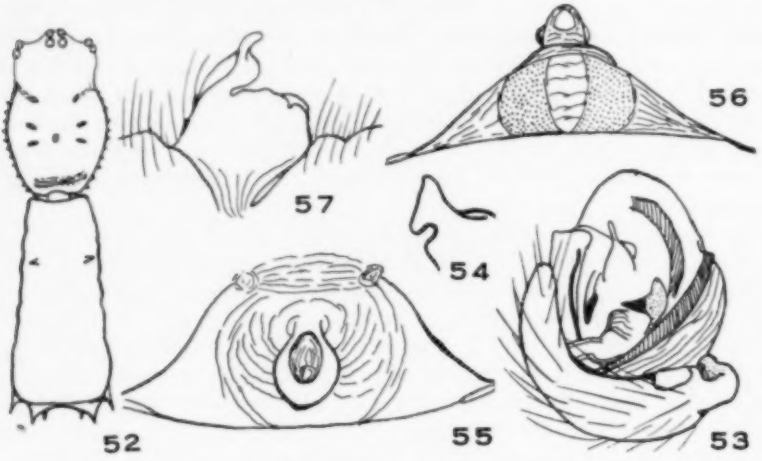
The male specimen described below was found with several females belonging to this species. For a time it was regarded as a representative of a new species but a closer study has convinced me that it is in reality the formerly unknown male of *M. henseli* Reimoser and is here described as such.

Male allotype. Total length from AME to tip of posterior spines 6·57 mm. Carapace 2·86 mm. long, 1·76 mm. wide opposite interval between second and third coxae where it is widest. Height of clypeus equal to slightly more than twice the diameter of AME.

Cephalothorax and *appendages.* Surface of carapace finely granulated and irregularly rugulose in posterior fourth ; head portion slightly raised and thoracic portion slightly raised behind the well developed median fovea ; with three pairs of inconspicuous dorso-lateral foveae ; finely serrated along ventral margin of carapace to head region ; with a low transverse ridge a short distance anterior to posterior margin. Sternum finely rugulose and with many setigerous tubercles ; only slightly convex ; continued between fourth coxae by a slender sclerite. With a moderately well developed hook on first coxa and a corresponding groove and ridge near the base of the second femur. All legs

more of less conspicuously spiny, especially the femora which also bear many setigerous tubercles. Features of the palp shown in Figs. 53 and 54.

Abdomen. General form as shown in Fig. 52 ; with four pairs of spines essentially as they occur in females of the species.



Figs. 52-57, *M. hensli*

52. Outline of body, allotype male, dorsal view. 53. Left palpal tarsus. 54. Palpal tarsal hook, more enlarged. 55-57. Eqigynum ; from below, posterior view, and right lateral view, respectively.

Colour in alcohol. Carapace a reddish brown, somewhat lighter on head and in central regions ; darker along the sides by virtue of presence of many black dots. Lip, maxillae, and chelicerae a rich dark reddish brown. Legs reddish brown with variations. Abdomen : dorsum with a series of yellowish white spots representing the continuous yellowish white dorsum of the female. The posterior spines are black.

Type locality. The jar from which the allotype was taken is labelled simply : Parana (Rogers). Presumably this is Parana, Brazil. Date of collection uncertain. From the Oxford Museum collection.

Note : It has been observed that females frequently do not show the small lower posterior spines. There is probably considerable variation in respect to spination in the species. The chief characteristics of the epigynum are shown in Figs. 55-57.

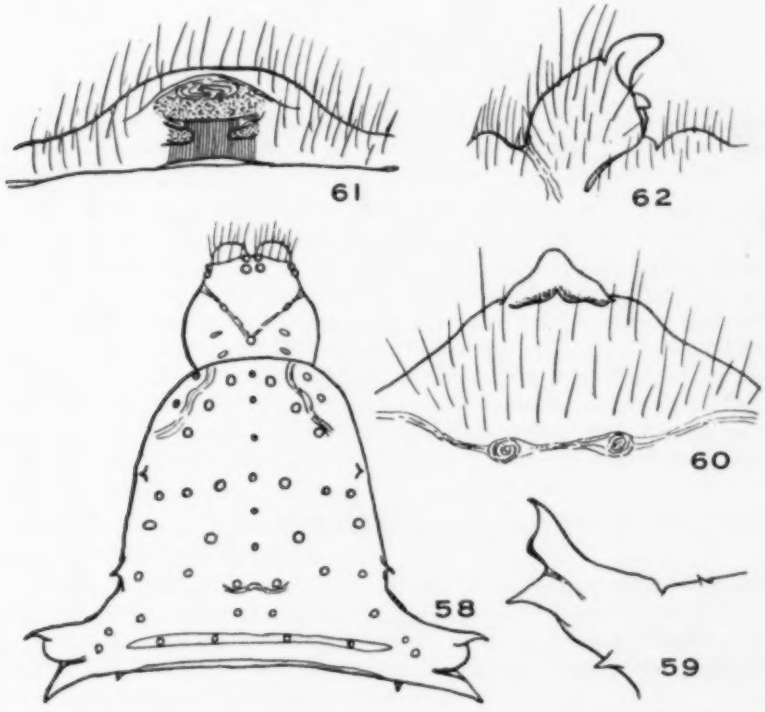
MICRATHENA HYATTI sp. n.

(Figs. 58-62)

Female holotype. Total length from chelicerae to tip of posterior spines 7·8 mm. Carapace 2·08 mm. long ; 1·82 mm. wide at level of second coxae where it is widest. Abdomen 5·4 mm. long from anterior border to posterior border exclusive of spines ; 7·85 mm. wide between tips of posterior spines ; 4·23 mm. wide just anterior to second pair of small lateral marginal spines. Height of clypeus about equal to diameter of AME.

Cephalothorax and *appendages*. Head moderately raised above thoracic portion of carapace and separated from the latter by a well defined groove ; central fovea well defined and circular ; carapace somewhat raised behind the central fovea ; with three pairs of dorsolateral foveae well developed. Sternum moderately convex ; with three pairs of small but distinct marginal tubercles and a single median posterior tubercle. All femora with many setigerous tubercles and fourth with numerous short spines.

Abdomen. General form as shown in Fig. 58. There are no anterior marginal spines ; there are two pairs of small lateral marginal spinules but the anterior pair of these are hardly more than low tubercles and are lacking on one paratype ; the posterior end is bifurcated and each fork is further divided into two large spines with a small spine beneath each fork ; there is a prominent swelling at the base of the dorsal of the two main spines. Epigynal features essentially as shown in Figs. 60-62. Observations on the epigyna of the two paratypes indicate that the general appearance of this organ may vary considerably in relation to the degree of internal tension in the abdomen.



Figs. 58-62, *M. hyatti* sp. n.
58. Outline of body, dorsal view. 59. Lateral view of spines, posterior end of abdomen. 60-62. Epigynum ; from below, posterior view, and right lateral view, respectively.

Colour in alcohol. Cephalothorax a medium brown with variations ; with a narrow dark stripe from PME to cephalothoracic groove. Sternum dark brown. Legs brown with variations. Abdomen : dorsum light reddish brown with variations ; with irregular white spots along middle ; posterior bifurcations much lighter.

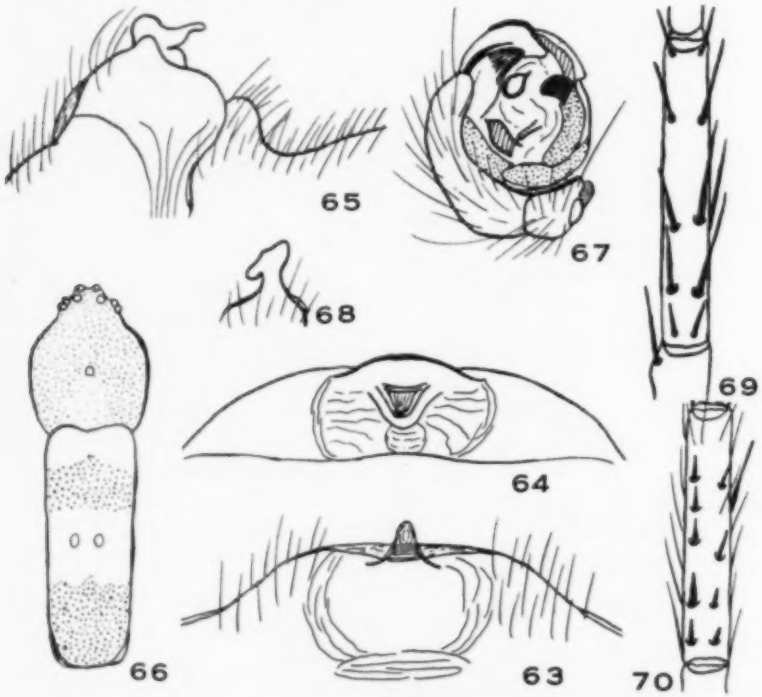
Type locality. Female holotype from St. Catherina, Humboldt, Joinville, Brazil ; October, 1916 (W. Ehrhardt, collection), Lord Rothschild. There is a single paratype from the same collection and another specimen from Rio Janeiro.

Holotype. Brit. Mus. (Nat. Hist.) 1921. 12.9.11 ; Paratype. Brit. Mus. (Nat. Hist.) 1921. 12.9.22.

MICRATHENA LUCASI (Keyserling), 1863
(Figs. 63-65)

Acrosoma lucasi, Keyserling, 1863 ; Keyserling, 1892. *Micrathena lucasi*, Simon, 1895 ; Petrunkevitch, 1911 ; Roewer, 1942 ; Bonnet, 1957.

Reimoser had no figures to accompany his description of this species which was taken from the original. Keyserling had one figure to show the dorsal side of the female. The male is unknown.



Figs. 63-65, *M. lucasi*
63-65. Epigynum, from below, posterior view, and right lateral view, respectively.
Figs. 66-70, *M. mansueta* sp. n.
66. Outline of body, dorsal view. 67. Left palpal tarsus. 68. Palpal tarsal hook, more enlarged. 69. First tibia, ventral view. 70. Second tibia, ventral view.

I have had an opportunity to study several specimens of this species in the British Museum (Natural History) collection. Some of them were pinned and dried at one time and later returned to alcohol with some injuries in the treatment. It has been thought to be worth while to select a lectotype and to indicate it as such in the collection. The chief features taken from this individual appear to be the following : Total length from AME to posterior border of abdomen 6·89 mm., to posterior end of posterior spines 8·45 mm. Distance between tips of posterior spines about as great as total length (somewhat broader than represented by Keyserling). The central thoracic fovea is well developed and circular ; there are three pairs of weakly developed dorso-lateral foveae, the first of which is deepest and in the cephalothoracic groove. The sternum is only moderately convex ; the seven tubercles mentioned by Keyserling are well developed. The abdomen has a pair of sharp spines arising from the anterior border, a pair of lateral marginal spines about two thirds the length of the abdomen ; the posterior end is bifurcated and each fork is divided into two short robust spines of about equal size by a horizontal plane. The carapace is not notably raised behind the central fovea. The lectotype is from Bogata, Columbia and is, apparently among the original lot studied by the author of the species.

MICRATHENA MANSUETA sp. n.
(Figs. 66-70)

Male holotype. Total length 4·55 mm. Carapace 1·82 mm. long ,1·38 mm. wide opposite interval between second and third coxae where it is widest. Height of clypeus equal to a little less than twice the diameter of AME.

Cephalothorax and *appendages.* Surface of carapace smooth with a sparse coating of fairly long light coloured hair ; central fovea well defined ; dorso-lateral foveae lacking. ME on a well defined tubercle with AME extended forward considerably. Sternum nearly flat and without well developed tubercles but a sclerite continues between posterior coxae. Promargin of fang groove with four small teeth and retromargin with three. Legs of normal length and general appearance ; markedly spiny ; tibia with ventral spines as shown in Fig. 69 ; second tibia with somewhat modified spines as shown in Fig. 70. Features of the palp essentially as shown in Figs. 67 and 68. First coxa with a hook and second femur with the corresponding ridge and groove on prolateral surface near proximal end. All legs with many bristles.

Abdomen. General form as shown in Fig. 66 ; very low posterior tubercles may represent suppressed spines.

Colour in alcohol. Carapace a rich reddish brown dotted with black except for a light area behind central fovea. Sternum reddish brown with black dots. Legs yellowish. Abdomen : dorsum nearly black in posterior region ; there is another dark band toward the anterior end thus leaving two light cross bands as indicated in Fig. 66.

Type locality. The jar from which this male came is simply labelled " Amazon " but it is assumed to have been a part of the collection from which the next species is derived : Collected by F. O. Pickard-Cambridge and E. E.

Austen from January to March, 1896 while on a trip of exploration on the S. S. Faraday.

Holotype. University Museum, Oxford. (Pickard-Cambridge Coll.)

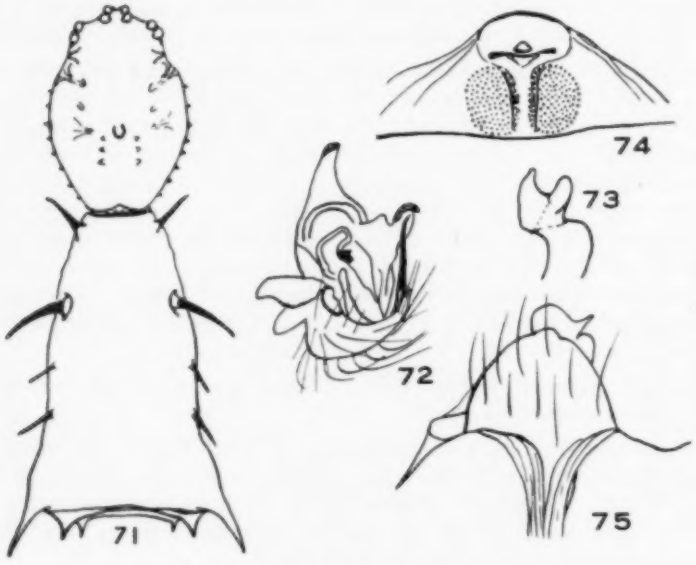
MICRATHENA NECOPINATA sp. n.

(Figs. 71-73)

Note : This specimen was for a time considered to belong to the genus *Chaetacis* Simon, 1895 but, after more careful study, it seemed to be closer to *Micrathena* and is, therefore, placed in that genus.

Male holotype. Total length from AME to tip of posterior spines 3·38 mm. Carapace 1·30 mm. long, ·91 mm. wide at level of second coxae where it is widest. Height of clypeus about equal to diameter of AME.

Cephalothorax and *appendages.* Carapace with a well defined central fovea and three pairs of dorso-lateral foveae decreasing in depth posteriorly ; with serrations along margin of carapace well defined in posterior half but suppressed in front of this ; with low tubercles and nearly suppressed denticles as indicated in Fig. 71 ; posterior part of carapace finely rugulose and granulated. Lateral-eyes almost in contact on moderately well-developed tubercles but medians hardly raised. Sternum moderately convex and granulated but not tuberculated. Legs moderately and normally spined but with no especially modified spination as in some other species. No coxal hook and no corresponding femoral ridge and groove observed. Setigerous tubercles are more or less



Figs. 71-73, *M. necopinata*

71. Outline of body, dorsal view. 72. Palpal tarsus. 73. Palpal tarsal hook, another view.

Figs. 74-75, *M. occidentalis*

74-75. Epigynum ; posterior and right lateral view, respectively.

conspicuous on third and fourth femora. Fang groove with teeth not readily observable because of fragility of specimen. Features of the palp are shown in Figs. 72 and 73. Only right palp found with specimen.

Abdomen. General form as shown in Fig. 71. The spines are retained in the male in this species with little or no reduction. There are seven pairs with their position and relative sizes as indicated. Anterior margin with several teeth which together with the contiguous thoracic border may constitute a stridulating apparatus.

Colour in alcohol. With varying shades of reddish brown ; dorsum lighter ; booklung areas dark brown. These colours may be faded from natural coloration.

Type locality. The male holotype is believed to have been collected along the Amazon River by F. O. Pickard-Cambridge and E. E. Austen while on a trip of exploration on the S. S. Faraday furnished by Siemans & Co., from January to March, 1896.

Holotype. University Museum, Oxford. (Pickard-Cambridge Coll.).

MICRATHENA OCCIDENTALIS (Taczanowski), 1879
(Figs. 74-75)

Acrosoma occidentalis, Taczanowski, 1879. *Micrathena occidentalis*, Simon, 1895 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

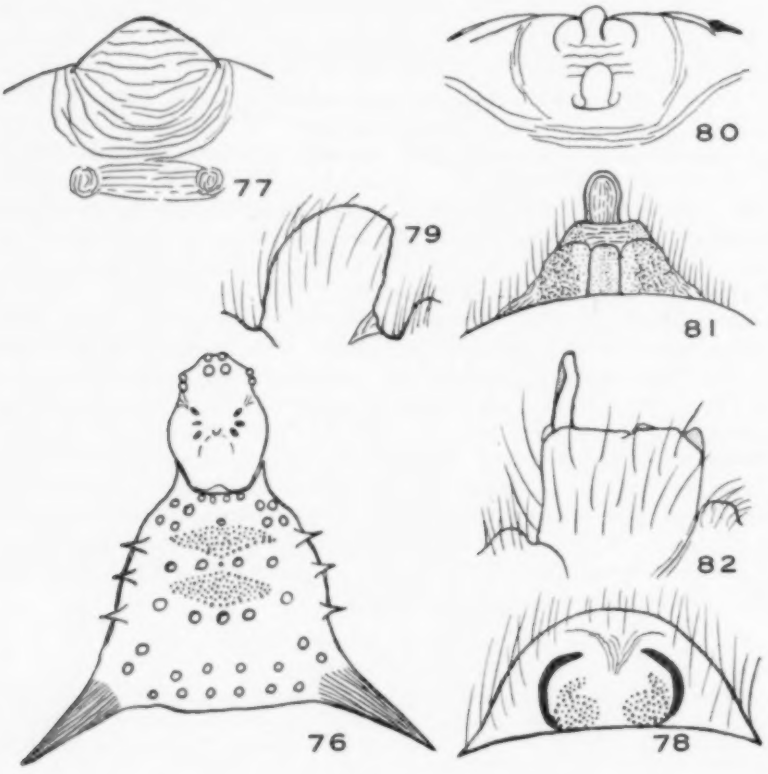
Only the female is known and this seems to have appeared in collections infrequently. One specimen in the Ehrhardt collection in the British Museum (Natural History) was available for study. The part of the collection from which this specimen came was dated : October, 1916, St. Catherine, Humboldt, Joinville, Brazil. Another specimen was available for study in the Museum of Comparative Zoölogy at Harvard College. This has no assigned date but is in the Reimoser collection from St. Catherina, Brazil. The original was from Peru. The unusual colour pattern appears to make identification quite certain (see Reimoser's Fig. 16). Figs. 74 and 75 are included here to show the chief features of the epigynum. Reimoser found only a pair of anterior spines ; the abdomen is bifurcate posteriorly and each fork is further divided into two spines by a nearly horizontal plane with the lower spine somewhat the longer. The Museum of Comparative Zoölogy specimen has another small spine on each side about one third of the length of the abdomen from the posterior border, thus again emphasizing variability.

MICRATHENA PUNGENS (Walckenaer), 1841
(Figs. 76-79)

Plectana pungens, Walckenaer, 1841. *Acrosoma pungens*, Keyserling, 1863 ; Keyserling, 1892. *A. luctuosa*, Taczanowski, 1873 (new synonymy). *Micrathena pungens*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957. *Micrathena luctuosa*, Petrunkevitch, 1911 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957.

There are two lots of these specimens in the British Museum (Natural History) separated out into two species, *M. luctuosa* (Taczanowski) and *M. pungens* (Walck). These have all been examined and compared with the result that I am compelled to regard them as belonging to the same species, *M. pungens* (Walck.). The most consistent difference between these two groups as they

have been separated seems to be the presence or absence of a small spine on each side just ventral to the large posterior spine. These have been found to be variable in several species studied by the author of this paper. A careful study of the numerous specimens of this species in the Museum of Comparative Zoölogy shows the following facts : the typical number of lateral marginal spines is three on each side ; but there may be a well developed tubercle on each side behind the third spine ; one of these may be erected into a spine so that there are three spines plus the tubercle on one side and four spines on the other side ; in a few cases, apparently, both tubercles may be erected into well defined spines so that there are four on each side. This belief prevented me from describing a new species with four spines on each side but with other features like those of ordinary members of *M. pungens* (Walck.).



Figs. 76-79, *M. pungens*

76. Body of female, dorsal view. 77-79. Epigynum, from below, posterior view, and right lateral view, respectively.

Figs. 80-82, *M. rubicundula*

80-82. Epigynum, from below, posterior view, and right lateral view, respectively.

The most important features for identification of the species appear to be the following : The colour pattern appears to follow that described by Reimoser (1917) quite consistently ; the size averages about 6 mm. in length ; general shape with spines essentially as shown in Fig. 76 ; the large posterior spines vary considerably in respect to direction and curvature ; the carapace has a well developed median fovea and moderately well defined three pairs of dorso-lateral foveae ; the carapace is moderately gibbous behind the median fovea ; sternum moderately convex and with a granular surface ; anterior lateral tubercles on sternum well marked, others only slightly developed ; posterior end of sternum with three small tubercles, not extended between fourth coxae ; epigynum as shown in Figs. 77-79. Female known from Guiana, Columbia, Brazil, Bolivia, and Peru. The male remains unknown.

MICRATHENA RUBICUNDULA (Keyserling), 1863

(Figs. 80-82)

Acrosoma rubicundula, Keyserling, 1863 ; Keyserling, 1892. *Micrathena rubicundula*, Simon, 1895 ; Reimoser, 1917 ; Roewer, 1942 ; Bonnet, 1957. *Micrathena rubicunda*, Petrunkevitch, 1911.

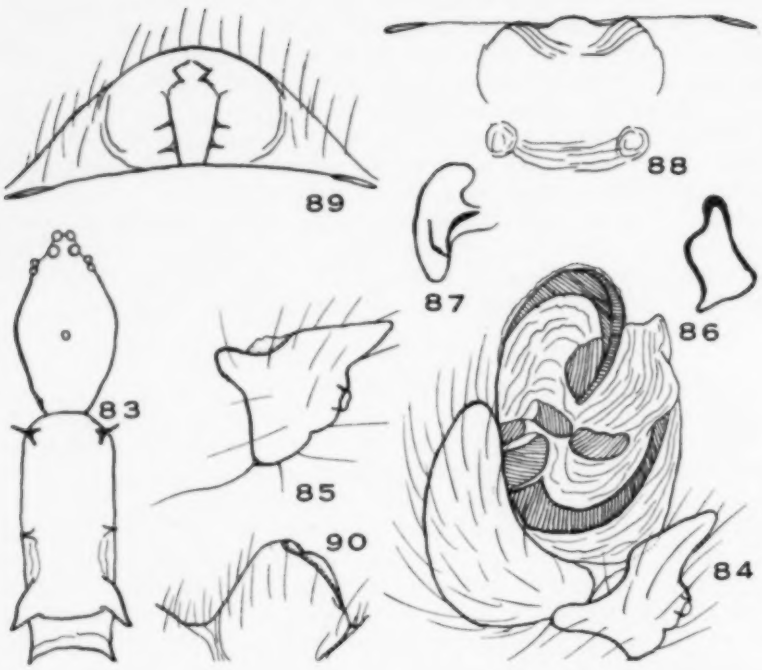
Keyserling published a detailed description of this species but included only a figure of the whole body from the dorsal surface. Reimoser (1917) borrowed directly from the original description and published no figures. I have studied specimens of this species in the Koch collection in the British Museum (Natural History) and offer the following facts as an aid to identification : Total length of the hypotype from AME to posterior border of abdomen 9·88 mm. ; length to tips of posterior spines 12·68 mm. ; the carapace has a fairly deep central fovea, is strongly gibbous behind the fovea and has a depression at the apex of the gibbosity ; the sternum is moderately convex and has weakly developed tubercles ; the abdomen has the six spines essentially as represented by the author of the species ; the chief features of the epigynum are shown in Figs. 80-82. Keyserling stated that he had six females from Columbia but now there are only two abdomens and a detached cephalothorax, all in poor condition, in the jar marked " types." Apparently known only from Columbia. The male is unknown.

MICRATHENA SWAINSONI (Perty), 1833

(Figs. 83-90)

Acrosoma swainsoni, Perty, 1833. *Acrosoma prudens*, Holmberg, 1887. *Micrathena prudens*, Simon, 1895 ; Petrunkevitch, 1911 ; Reimoser, 1917. *Micrathena swainsoni*, Petrunkevitch, 1911 ; Reimoser, 1917. *Micrathena paraguayensis*, Mello-Leitao, 1931. *Micrathena silvicola*, Badcock, 1932 (new synonymy)

There are several good specimens of this species in the British Museum (Natural History). These have all been studied and carefully compared with the types of *M. silvicola* Badcock, 1932 with the result that I am obliged to place the latter as a synonym of the former. Figures of the holotype and allotype of *M. silvicola* have been prepared for comparison with the published figures of *M. swainsoni* (Perty). The species is now known from numerous widely separated regions of South America. It may be noted that this is another species in which spines are retained in the adult male much as in the female.



Figs. 83-90, *M. swainsoni*

83. Outline of male, dorsal view. 84. Left male palpal tarsus and tibia. 85. Left male palpal tibia ; slightly different view. 86. Distal end of palpal tarsal hook ; more enlarged. 87. Lateral view of palpal tarsal hook. 88-90. Epigynum ; from below, posterior view, and right lateral view, respectively.

ACKNOWLEDGMENTS

Acknowledgments are due and gratefully rendered to the following named individuals and organizations for their many courtesies, support and encouragement of my work for many years : The John Simon Guggenheim Memorial Foundation for its support of my work during the past two years ; Dr G. Owen Evans, Department of Zoölogy, British Museum (Natural History) and his staff of co-workers all of whom gave me very friendly encouragement and the loan of important sepcimens for the pursuit of my work ; Professor G. C. Varley and his staff of co-workers at the Oxford University Museum who gave me access to valuable specimens for a brief period and then extended material on loan to help me further ; Dr A. S. Romer, Director, Dr P. J. Darlington, Jr., Curator of Insects, Dr Herbert W. Levi, Associate Curator of Arachnology, and Miss Nelda E. Wright, Editor of Publications, all of the staff of the Museum of Comparative Zoölogy at Harvard College.

REFERENCES

BADCOCK, A. D. (1932). Arachnida from the Paraguayan Chaco. *J. Linn. Soc., Lond.* (Zool.) **38** : 1-48.

BONNET, P. (1957). *Bibliographia araneorum.* **2.** 3me partie. Toulouse : Les Artisans de l'Imprimerie Douladoure,

KEYSERLING, GRAF E. VON. (1863). Beschreibung neuer und wenig bekannter Arten aus der Familie. Orbitelae Latrl : oder Epeïridae Sund. *S. B. Nat. Ges. Isis Dresden* **1863:** 63-98 ; 119-154.

KEYSERLING, GRAF E. VON. (1892). *Die Spinnen Amerikas.* **4** *Epeiridae.* Nürnberg V : von Baur & Raspe.

REIMOSER, E. (1917). Die Spinnengattung Micrathena. *Verh. zool. bot. Ges. Wien* **67** : 73-160.

ROEWER, C. FR. (1942). *Katalog der Araneae.* **1.** Bremen : Kommissions-Verlag von " Natura ".

SIMON, EUGENE. (1892-1903). *Histoire naturelle des Araignées.* 2nd Edition. 2 Vols. Paris : Librarie Encyclopedique de Roret.

BLOOD STUDIES ON THE ECHIDNA *TACHYGLOSSUS ACULEATUS*

BY

A. BOLLIGER, PH.D., D.SC., F.R.A.C.I.
Gordon Craig Research Laboratories, Department of Surgery
and
T. C. BACKHOUSE, M.B., B.S., D.T.M.&H., F.R.A.C.P.
School of Public Health and Tropical Medicine, University of Sydney

[Communicated by Dr J. R. Simons F.Z.S.—Accepted 9th February 1960]

(With 1 plate and 3 tables in the text)

The blood picture of the echidna *Tachyglossus aculeatus*, one of the two monotremes still extant, was studied on forty-two apparently healthy and diseased specimens.

In spite of the reptilian and avian attributes, the red and white cell characteristics and counts, response to infection, etc. of this prototherian correspond typically to those of higher mammals.

Compared with Eutheria the average "normal" haemoglobin content was high (17·4 gram per cent). Nucleated red cells were only observed in marked anaemia and reticulocytes were almost never seen. The prevailing polymorph was a mature neutrophil. Eosinophils were uncommon and basophils rare and then only in disease.

A varying degree of piroplasmosis was present in most of the animals examined. This did not have a definite influence on the blood picture if light or moderate. The haemoglobin content diminished considerably if the echidna was kept in captivity for more than two months.

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INTRODUCTION

During an investigation of a newly described babesioid parasite (*Babesia tachyglossi*) in the erythrocytes of a monotreme, the echidna or spiny anteater *Tachyglossus aculeatus* (Backhouse & Bolliger 1957, 1959) smears of the blood from forty-two echidnas were examined. To our knowledge this is the first time that the blood of monotremes has been examined from such a large number. The examination enables us to make some useful generalizations about the blood of these animals. In addition to the examination of the formed blood elements we also made some counts of both red and white blood cells as well as a considerable number of haemoglobin determinations.

HAEMOGLOBIN

Haemoglobin was determined by the ammonia method (see Wintrobe, 1956) and the resulting colour was read in a photoelectric colorometer which had been previously calibrated. A total of fifty-three haemoglobin determinations were performed on twenty-six echidnas of varying ages and sexes, twenty-four of which exhibited a piroplasmosis of widely differing degrees. The results ranged from 10·4 to 20 gram of haemoglobin in 100 mls. of blood. This does not represent a normal range because some of the echidnas examined were obviously not healthy and we have strong reasons for believing that at least five of the reported haemoglobin values below 13·8 gms are abnormally low. They were obtained from five animals, four of which presented signs of disease such as haemorrhage or severe infection. The fifth echidna had been submitted to splenectomy a few weeks prior to haemoglobin determination. The remaining forty-seven haemoglobin values of twenty-two echidnas ranged from 13·8 to 20 grams, averaging 17·1 grams. In order to establish an approximately normal range of haemoglobin values thirteen echidnas were selected which had lived in captivity less than four weeks, which were bled for the first time,

TABLE 1

Blood counts on 13 "normal" echidnas. Note the high haemoglobin content, the absence of basophils and the scarcity of eosinophils.

No.	Hgb.	R.B.C.	W.B.C.	N.	E.	B.	L.	Mo.	M.C.H.
4	16·5	6·9	8·7	12	0	0	87	1	23
11	16·7		6·6	40	0	0	57	3	
12	17·6	7·0	9·9	44	0	0	54	2	25
13	17·6	7·3		28	0	0	68	4	23
18	18·4			24	1	0	74	1	
19	16·6	6·9	5·0	15	0	0	84	1	24
24	18·6		7·6	32	0	0	67	1	
29	17·8								
31	17·5	7·5							22
32	19·4	9·2							21
34	16·6	6·8							24
36	16·5	7·0	7·8	34	0	0	65	1	24
40	17·5	7·0							25
Mean	17·4	7·3	7·6	29	0·1	0	69	1·8	23

For abbreviations see Table 2.

which showed no obvious disease or injury and which were not infected by piroplasmosis, or only moderately so, the number of erythrocytes infected not exceeding 1 per cent. The results of these thirteen haemoglobin determinations ranged from 16·5 to 19·4 grams per cent averaging 17·4 grams per cent (Table 1). In subsequent determinations performed within one to three weeks on the same animal similar values were obtained provided the echidna had remained in fair health. This would indicate that the haemoglobin content of echidna blood is higher than that encountered in most other mammals (Wintrobe 1956).

Echidnas kept in captivity over several months have a haemoglobin content 1 to 6 gram per cent lower than the " normal range ". This is demonstrated in echidna 22 kept for nine months (Table 3) under experimental conditions. The average haemoglobin content during this period was 15·2 grams per cent. For the first six months this specimen exhibited marked persistent piroplasmosis including a short unexplained period of anaemia characterized by low haemoglobin as well as the appearance of 2 per cent of nucleated red cells in the blood (see determinations of 2.4.1958). The administration of penicillin for the treatment of a pyogenic infection markedly diminished the piroplasmosis. This had no significant effect on the haemoglobin level.

ERYTHROCYTES

Briggs (1936) examined the red blood corpuscle of the *Tachyglossus* and found it to be a non-nucleated biconcave disc in conformity with its mammalian characteristics. This was further confirmed on our big range of Leishman stained material from forty-two echidnas. The diameter of these discs was approximately that of a human erythrocyte. Nucleated red cells in the form of normoblasts were seen only when the haemoglobin content was at least 4 grammes below the average normal value. The appearance of these immature forms of erythrocytes in anaemia would further confirm the mammalian nature of the red corpuscles of the echidna. Anisocytosis was also noticed under similar conditions. After staining with brilliant cresyl blue only one reticulocyte at a haemoglobin level of 10 gram per cent was seen in the numerous specimens examined.

Red cell counts were performed on nine echidnas with apparently normal blood haemoglobin values (16·5 to 19·4 gram per cent). The red cell counts were correspondingly high (6·8 to 9·2 millions per cmm) and the mean corpuscular haemoglobin content varied from 21 $\gamma\gamma$ to 25 $\gamma\gamma$ (average 23 $\gamma\gamma$). In echidna 22 (Table 3) after having been kept in captivity for six months and after numerous small blood lettings the mean corpuscular haemoglobin content was 28 $\gamma\gamma$ at a haemoglobin content of 15 gram per cent. Values for the size and haemoglobin content of the red corpuscles of an animal bled by heart puncture after one, seven and eight months of captivity are shown in Table 2.

LEUCOCYTES

Morphologically the granular leucocytes are of the mammalian polymorpho-nuclear type. The neutrophils show a marked shift to the right, that

is to say they show a larger number of lobes than is usually found in man. In proportion, however, the neutrophils are not as numerous as in human blood and a relative lymphocytosis is normally present ; a condition seen in many mammals. In the absence of infection less than 50 per cent and sometimes as few as 10 per cent of the leucocytes are neutrophils. In the presence of infection neutrophils increase to over 50 per cent and have been found to be 90 per cent of the total leucocyte count. The relative number of neutrophils falls again below 50 per cent with the disappearance of the infection. This is demonstrated in echidna 22 (Table 3) which developed an abscess on one of the hind legs. At this stage the polymorph count was 65 per cent but dropped again to less than 50 per cent after successful treatment of the infection by drainage and penicillin administration. The total leucocyte count, normally between 5000 to 10000 cells per c.mm reveals comparable trends, i.e. rise in response to infection.

TABLE 2

Echidna 42. Bodyweight 2·1 kg. slightly infected by *Babesia tachyglossi*. Blood counts on heart blood taken during the first, seventh and eight month of captivity. With each heart puncture 15 ml. of blood were removed. Note the progressive anaemia.

Date	16.10.58	14.5.59	17.6.59
Hgb.	18·5	14·2	11·0
R.B.C.	8·1	5·4	4·8
Ht.	5·2	4·5	3·7
M.C.V.	74	84	77
M.C.H.	23	26	23
M.C.H.C.	32	32	29
W.B.C.	7·8	5·5	7·2
N.	32	31	53
E.	0	0	2
B.	0	0	0
L.	67	66	42
Mo.	1	3	3
Pl.	300	320	

Abbreviations : Hgb., haemoglobin in grams per 100 ml. blood ; R.B.C., red cell count in millions per c. mm. ; Ht., volume of packed red cells in ml. per 100 ml. ; M.C.V., mean corpuscular volume in cubic microns ; M.C.H., mean corpuscular hemoglobin in micromicrograms ; M.C.H.C., mean corpuscular hemoglobin concentration in per cent ; W.B.C., leucocyte count in thousands per c. mm. ; N., neutrophils ; E., eosinophils ; B., basophils ; L., lymphocytes ; Mo., monocytes all in per cent ; Pl., platelets in thousands per c.mm.

TABLE 3

BLOOD STUDIES ON ECHIDNA No. 22 Body weight 2·3 kg.

Note essentially "normal" findings in spite of marked parasitaemia till a pyogenic infection occurred at the hind legs where blood was obtained. This produced a temporary leucocytosis and increase in neutrophils. Treatment with penicillin injections proved successful. Simultaneously the number of parasites was drastically reduced. For abbreviations see Table 2.

Date	Hgb	RBC	WBC	N.	E.	B.	L.	Mo	R.B.C.% Parasitized	Remarks
1957										
10.10	16·8	7·0	7·8	13	0	0	85	2	6	Healthy appearance
16.10				41	0	0	58	1		
18.10				40	0	0	59	1		
4.11	15·7								11	
27.11	15·2									
20.12				41	1	0	57	1	7	
1958										
3.3	16·6			47	0	0	51	2	22	
17.3	17·4									
2.4	12·6			30	0	1	68	1	25	2 nucleated R.B.C. % W. B. C. Basophile
9.4	14·1	5·0	10·0	38	0	0	60	2	29	
16.4	15·0	5·3	7·0	47	0	0	50	3		
24.4	16·0		6·5							
1.5	15·0		7·0	45	0	0	52	3	15	
8.5	15·5		14·0	65	0	0	34	1	19	Pyogenic Infection 200,000 U. penicillin
16.5	15·5		13·1	60	0	0	39	1		Pyogenic Infection 200,000 U. penicillin
27.5	13·9		8·8	49	0	0	50	1	0·1	Infection clearing 200,000 U. penicillin
5.6	16·6									Infection clearing 200,000 U. penicillin
11.6	13·8		7·9	44	0	0	54	2	0	Normal
2.7	14·9		8·4	41	0	0	55	4	$<0·05$	,,
9.7	15·2		6·1	39	0	0	60	1	$<0·05$	,,
21.7	15·7		9·3						$<0·05$	,,
5.8	14·6		10·2	41	0	0	58	1	$<0·05$	,,

In the "normal" echidna there is a definite tendency for the leucocyte picture to remain simple i.e. mature neutrophils and lymphocytes and comparatively few monocytes. Eosinophilic leucocytes for example occurred in smaller numbers than reported for higher mammals (Wintrobe, 1956) and in some specimens no eosinophils were encountered even after counting 500 white cells. One or two basophils were seen only in anaemic echidnas. So-called "drum sticks" could also be observed but could not be related to the sex of the animal because in one instance they were present in a number of polymorphs from a male echidna. (Undritz, 1958).

ACKNOWLEDGMENTS

We wish to thank Dr H. Kronenberg, Haematologist, Fairfax Institute of Pathology, Royal Prince Alfred Hospital, Sydney, and his staff for assistance with a number of blood counts. We are also indebted to Sir Edward Hallstrom for his kind permission to examine echidnas at the Taronga Park Zoological Gardens.

ADDENDUM

The care of the echidna and the taking of blood specimens.

In reply to a number of enquiries about keeping echidnas in captivity we would like to point out that with proper care the anteater can be kept in the laboratory for many months or even years.

On account of its powerful muscles and digging feet and its stout spiny covering (Pl. 1, fig.1) a plain room without objects into which the animal can wedge itself, was found most suitable provided the floor is covered with sawdust which in part should be about 6 inches deep, or by a pile of woodwool or straw, which has to be renewed at least once a fortnight.

It is obviously difficult to give the toothless echidna in captivity its natural food such as termites, their eggs, larvae, etc. However, a diet of milk, eggs and meat finely homogenized in a blender seems to be adequate. About once a week the animal should be taken into a paddock where it can dig and procure some of its natural food. Constant supervision is necessary otherwise the animal may burrow into the ground and be lost.

Usually if one picks up an echidna it rolls itself into a ball, protected all around by sharp quills. However, by taking hold of the claws of the hind legs, which is usually not difficult, and letting the animal hang in a vertical position, small blood samples may be obtained by puncture or by a small incision through the skin of the dorsal surface of the lower leg. It is advisable to close the incision with a suture.

Tachyglossus can be readily immobilized by means of a thin board (40 x 20 cm.) which contains a circular opening of about 4 cms. in diameter. A strap with a buckle is fixed about 15 cms. from the opening. The animal is picked up by a hind leg and the noose of the leather strap is attached to the hind leg directly above the claws. Both the leather strap and the leg to which it is attached are threaded through the opening in the board. The leg is extended by pulling the leather strap which is then secured tightly in the buckle. (Pl. 1, fig. 2). By pressing the board against the laboratory table

Fig. 1.—The ventral surface of the echidna. Note the powerful claws. By taking hold of the claws of the hind legs and letting the animal hang in vertical position small blood samples may be obtained by puncture or incision through the skin of the hind legs.

Fig. 2.—Immobilising the echidna for taking blood. The leg attached to a strap is pulled through an opening in a board and the strap is fixed in a buckle. In this picture the leg is not fully pulled through the opening in order to show the dorsal aspect of the animal.

the echidna is prevented from moving and blood samples sufficient for total blood count and some micro-chemistry may be readily obtained simply by cutting through the skin. Blood specimens of about 15 mls. or more can be obtained by cardiac puncture of the anaesthetized echidna.

REFERENCES

BACKHOUSE, T.C. & BOLLIGER A. (1957). A piroplasm of the echidna (*Tachyglossus aculeatus*). *Austral. J. Sci.* **20** : 24-25.

BACKHOUSE, T. C. & BOLLIGER, A. (1959). *Babesia tachyglossi* n. sp. from the echidna *Tachyglossus aculeatus*. *J. Protozool.* **6** : 320-322.

BRIGGS, E. A. (1936). The red blood corpuscles of primitive mammals. *Nature, Lond.* **138** : 762.

UNDRITZ, E. (1958). *Personal communication.*

WINTROBE, M. W. (1956). *Clinical hematology.* London : Kimpton.

THE METABOLISM OF SOME BRITISH SHREWS

BY

A. E. HAWKINS, PH.D., F.INST.P.,
P. A. JEWELL, PH.D., F.Z.S. AND GILLIAN TOMLINSON

Department of Physiology, Royal Veterinary College
University of London

[Accepted 9th February, 1960]

(With 2 figures in the text)

The metabolism of some British shrews was determined and compared with that of laboratory mice. The results obtained indicated that the metabolism of the shrews was not higher than was to be expected on the basis of size alone.

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INTRODUCTION

It has been shown by Morrison & Pearson (1946) and by Pearson (1947,1948) that the oxygen consumption when resting (i.e. still, but not post-absorbtive) of various American shrews is well above that of various wild mice and voles of the same weight ; and also that the smallest mammals examined (*Sorex cinereus* and *Sorex vagrans vagrans*) have an oxygen consumption even higher than could be predicted from the other shrew values on the basis of size alone. On the other hand, Redmond & Layne (1958) in *in vitro* experiments have found that the metabolic rates of certain tissues of the American shrew *Cryptotis parva* are not higher than could be predicted on the basis of size alone, and they suggest that the high rates of oxygen consumption exhibited by the shrews used by Pearson must be due to extrinsic factors, such as nervous stimulation, rather than to higher inherent rates of tissue metabolism.

MATERIAL AND METHODS

Both a manual (Clarke & Hawkins, 1956) and an automatic (Hawkins, 1958) differential calorimeter were in use in this laboratory at a time when some shrews became available and the opportunity was taken to measure their rate of heat loss. Both forms of apparatus enable the rate of heat loss to be determined in a particular state of activity ; values were obtained for one *Sorex minutus*, one *Sorex araneus*, one *Crocidura cassiteridum* and two *Neomys fodiens bicolor*. In each case values were recorded for the three states : rest, head movements only and locomotor activity. Since shrews appear to groom very rarely and then only for a very short time, no entirely satisfactory values were obtained for grooming.

The shrews were housed in glass tanks at an ambient temperature of 18-20° C, and when in the calorimeters were at an ambient temperature of 28-30°C, that is within the zone of thermal neutrality for mice. The rates of heat loss of growing mice of a grey strain were used for purposes of comparison. These were kept at an ambient temperature of 20°C. Each experiment provided several values for each activity state ; a period of about thirty minutes sufficed for the mice but a period of sixty minutes or more was necessary for the shrews. Larvae of blowflies provided the food supply for the shrews whilst in the calorimeters.

RESULTS

The results for resting mice and shrews are shown in logarithmic form in Fig. 1. These results were obtained from one hundred experiments for mice during which the mouse was still for several minutes on at least two occasions, and from about twenty experiments under the same conditions for the shrews.

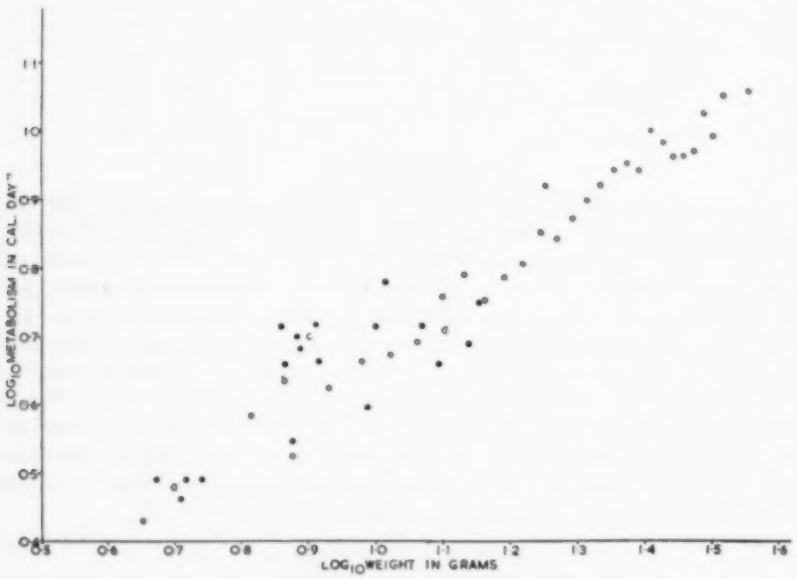

Fig. 1.—Log_{10} (metabolism in Cal. day^{-1}) plotted against log_{10} (weight in grams) for resting mice and shrews.

○ = mice ; ● = shrews

(a = *Sorex minutus*, b = *Sorex araneus* (4 lower points), c = *Crocidura cassiteridum*, d = *Neomys fodiens bicolor*)

In most cases the values for mice are the averages of at least four experiments. The shrew determinations are plotted individually, those for *Crocidura cassiteridum* were difficult to obtain and are probably too high, since the shrew was rarely still and then only for a minute or so at a time.

It is clear from Fig. 1 that there is no apparent difference in the rates of heat loss in the resting state between the shrews and mice of the same weight. Similar results have been obtained in the other two activity states which have been considered and Fig. 2 illustrates the results for locomotor activity. Here sufficient readings were obtained for average values for each shrew at a

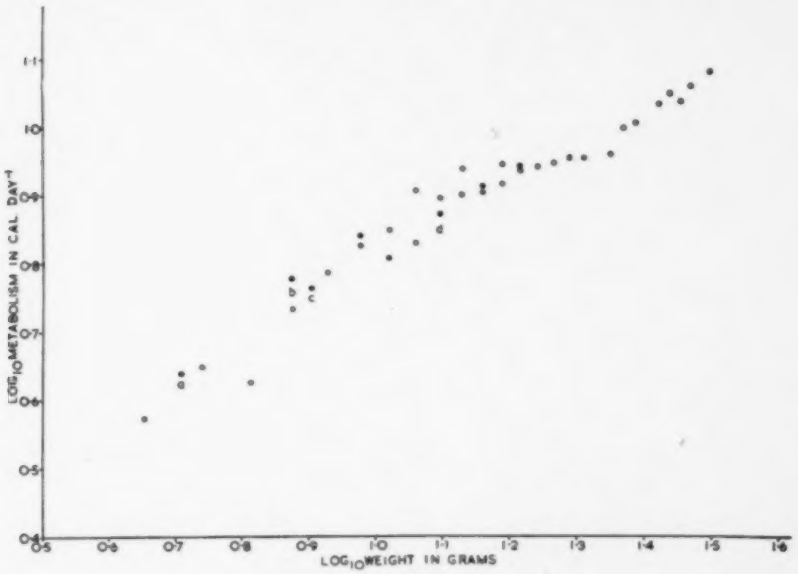

Fig. 2.—Log_{10} (metabolism in Cal. day^{-1}) plotted against log_{10} (weight in grams) for mice and shrews exhibiting locomotor activity.

○ = mice, ● = shrews

(a = *Sorex minutus*, b = *Sorex araneus*, c = *Crocidura cassiteridum*, d = *Neomys fodiens bicolor*)

given weight to be plotted, and most of the mice figures are averages of seven or more experiments. Provided there is not a large difference between the surface area/volume ratio for shrews and for mice this equality in rate of heat loss is to be expected, since Kendeigh (1945) and Pearson (1948) have found no difference in body temperatures of American shrews and mice, and Hawkins and Jewell (unpublished data) found none in a preliminary experiment on small British mammals. It is evident, therefore, that if the body temperatures, the metabolic rates of the tissues, and the rates of heat loss are the same, then the rates of heat production should be the same.

The rates of heat production of the specimens of the four species of shrews have been determined using a gravimetric calorimeter of the Haldane type. (Haldane, 1892). This apparatus yields an average value over a period of time of the order of an hour, and it has only been found possible to obtain values for a state approaching the resting condition for the specimen of *Sorex minutus*. This was made possible because this shrew would sometimes eat a

maggot and then sit still for most, if not all, of an hour. The mice and the remaining shrews never behaved in this manner. It was fortunate that *Sorex minutus* was the quietest shrew since the resting value for this, the smallest of the British shrews, is the most critical. In order to calculate heat production from the figures of CO_2 production, since it is almost impossible to obtain an exact measure of the R.Q. with a gravimetric calorimeter, an R.Q. of 0·82 was assumed as recommended by Brody (1945). The average values of 10 R.Q. determinations were respectively grey mice 0·78 ; albino mice 0·81 ; *Neomys fodiens bicolor* 0·81 and *Crocidura cassiteridum* 0·82.

The values obtained for the rate of heat production of *Sorex minutus* are given in Table 1. These were obtained at a chamber temperature of approximately 26°C. If these values are compared with those calculated from Pearson's figures for *Sorex vagrans vagrans* of approximately the same weight, it will be seen that those for *Sorex minutus* are lower. The lowest values are in fact,

TABLE 1

Rate of heat production of the shrew *Sorex minutus* and the values calculated from O. P. Pearson's results for the shrew *Sorex vagrans vagrans*.

Species	Weight (gram)	Heat Production (Calories day^{-1})	
		Air	Oxygen
Sorex minutus	4·2	4·3	—
	4·5	4·4	—
	4·7	—	3·9
	4·7	—	4·1
	4·9	—	4·2
	5·6	3·6	—
Sorex vagrans vagrans	4·5	—	4·5
	5·1	—	4·7
	5·4	—	4·6

those to be expected from the values for wild mice and voles calculated from Pearson's results obtained at the same chamber temperature. Higher values (5·0, 5·1, 5·3, 6·5, 6·8, 7·3 Cal. day^{-1}) were also obtained for *Sorex minutus* but it is known that the shrew was only in a state of rest for a part of the hour.

The fact that air was used in the present experiments whereas Pearson used oxygen, might be significant since Harvey (1958) has shown that with guinea pigs the addition of oxygen to air appears to produce a higher metabolism in the resting state. However, as is shown in Table 1 there is no evidence of such an effect with *Sorex minutus*, and switching from air to oxygen or vice versa, whilst operating the differential calorimeter, produced no measurable effect on the rate of heat loss of mice or of shrews.

COMMENT

Certain factors entered into the experiments which might account for the values obtained for the metabolism of resting shrews being more predictable

than those of Pearson. The shrews were accustomed to laboratory conditions and had food ad lib.; they were not handled directly, but were transported in nesting tubes kept in their living quarters. The tubes were similar to those used in the calorimeters and the shrews merely walked from one chamber to the other at the beginning and end of an experiment. The animals were thus in an almost undisturbed state when the measurements were carried out.

ACKNOWLEDGMENTS

The authors are indebted to Mr I. Linn for the loan of the specimen of *Crocidura cassiteridum*, and one of us (A. E. H.) gratefully acknowledges a grant from the Central Research Fund of the University of London.

REFERENCES

Brody, S. (1945). *Bioenergetics and growth*. New York.

Clarke, E. G. C., & Hawkins, A. E. (1956). A simple differential calorimeter for small animals. *Phys. in Med. Biol.* **1** : 118.

Haldane, J. S. (1892). A new form of apparatus for measuring the respiratory exchange of animals. *J. Physiol., Lond.* **13** : 419.

Harvey, D. G. (1958). The measurement of oxygen consumption in small animals. *J. Pharm., Lond.* **10** : 483.

Hawkins, A. E. (1958). A self-adjusting unit for the control of an animal calorimeter. *J. sci. Instrum.* **35** : 440.

Kendeigh, S. C. (1945). Body temperature of small mammals. *J. Mammal.* **26** : 86.

Morrison, P. R. & Pearson, O. P. (1946). Metabolism of a very small animal. *Science, N.Y.* **104** : 287.

Pearson, O. P. (1947). The rate of metabolism of some small mammals. *Ecology* **28** : 127.

Pearson, O. P. (1948). Metabolism of small mammals, with remarks on the lower limit of mammalian size. *Science, N.Y.* **108** : 44.

Redmond, J. R. & Layne, J. N. (1958). A consideration of the metabolic rates of some shrew tissues. *Science, N.Y.* **128** : 1508.

ON SOME SUNDRY SPECIES OF SOLIFUGIDS IN THE COLLECTIONS OF THE HEBREW UNIVERSITY OF JERUSALEM

BY

F. A. TURK

Reskadinnick, Camborne, Cornwall

[Accepted 9th February, 1960]

(With 10 figures in the text)

This paper deals with those species of solifugids, not themselves occurring in Israel, which are preserved in the collections of the Hebrew University of Jerusalem. The difficulties of finding valid characters for the differentiation of species and genera within the Order are discussed and a new classification of the family Galeodidae is proposed based on the observed fact that the distal spinulation of the tarsi is more constant than the proximal : in pursuance of this *Paragaleodes* Kraepelin is brought back into use. A discussion of the specific characters of the Galeodidae follows and Birula's work on the use of differentiated stridulatory setae is amplified and three types of these are recognized. Five new species of galeodids are described as well as a new genus and species of Solpugidae from Kenya. In addition new species of Rhagodidae and Daesiidae are described and new records of the occurrence of species of the families Karschiidae and Ammotrechidae are noted.

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INTRODUCTION

Through the kindness of Professor Theodor, Dr Shulow and Dr Wahrman I have, over the past five years, been able to examine all the specimens of solifugids in the very extensive collections of these somewhat rare animals which are housed in the zoology collections of the Hebrew University of Israel. The very rich and interesting solifugid fauna of Israel naturally forms the greatest bulk of these collections and includes many of the type and homeotype specimens examined by Professor Roewer, in the course of his studies for his great monograph on the group and the supplement (Roewer 1932-1934 and 1941). Besides this material however there are other specimens, which have accumulated

over the course of the years, which come from countries outside Israel and it is these which form the subject matter of the present paper. The solifugid fauna of Israel itself will form the subject for a monographic treatment which it is purposed to publish elsewhere and for which I have now completed all the preliminary studies.

At the present moment solifugid studies are in a somewhat chaotic state : although some 750 to 800 species of these animals have been described from the arid and semi-arid regions of the world it is often difficult to be sure of the identity of a specimen since almost nothing is known of specific variation and its extent in many groups, still less is known of the geographical range of many and the generic distribution has, in part, proved to be wildly inaccurate. The causes of this are two fold ; firstly, in many groups there is only a very limited number of characters that can be used for classificatory purposes and this is particularly so for the female sex which is usually much more commonly found ; secondly, the system inaugurated by Roewer made use almost exclusively of the number of tarsal segments and of their spinulation. My own studies have convinced me that, although the first of these is valid in most families yet it needs to be used with caution in the extensive family of the Daesiidae and, with regard to the use of spinulation formulae there has been a growing feeling among several workers that this was completely untrustworthy for generic differentiation especially in the three families of the Galeodidae, Solpugidae and Rhagodidae. Although later authors, including myself, have continued to use the system of generic differentiation used by Roewer this has been solely on account of the convenient frame of reference which it provides and not because it was thought to provide anything like an approach to a natural system of classification ; indeed, it may be thought that the " coup-de-grace " to much of the system of Roewer was given in the short but very important paper of Panouse (1950).

A further difficulty arises in some groups in connection with the identification of females and as this is the predominant sex in any collection the difficulty is tantamount to imposing a considerable handicap on the systematic study of this group of arachnids. Dr R. F. Lawrence says (in litt. 24 vi. 1957) that he often avoids naming the females of the Daesiidae and Galeodidae because of the uncertainty attending the use of Roewer's keys to this sex and this matter is further complicated by the fact that it is almost certain that in some families the males and females of the same species are described under different specific names ; I have indeed myself found, during the examination of material in the collections of the Hebrew University, in specimens determined by Professor Roewer himself, that among those labelled " *Galeodes arabs* Linn. ♀ " were included females of *Galeods lacertosus* Roewer 1934, a species previously known from the male sex alone.

With these pitfalls in mind, and since of necessity in this Order many species have to be found on the critical examination of a single specimen—and that often in families where the expected range of variation (although, fortunately, experience shows this to be usually very small) is not known—I have thought it best to give more extended descriptions of new species than is usual with many authors. This is done not only to fix the type with greater

exactitude but because it will be easier in the future to study the ecological and geographical relations of species of solifugids if this is done : these relations between species are made difficult to study by the fact that in many families, in the females especially, the variant characters known are so few. Apart from the descriptions of new species I have added records of other known species or even of a generic attribution where this extends the range at present known for either the species or the genus.

Following the hitherto accepted practice I have added in the descriptions of new species a detailed account of the colour pattern since experience shows this to be remarkably constant for most of the Galeodidae and the Rhagodidae although it is probably less reliable in the other families. Since also, an accepted system of English equivalents for the German terms applied to various characters is much to be desired I have utilized those suggested by Whittick (1939) and by myself (Turk 1947) to which I have added one or two more as they seemed necessary ; the bare list of equivalents may be very briefly set out here for convenience without the accompanying definitions :—

Zwischenzähne = Intermediate-teeth
Zylinderborsten = Cylindrical-bristles
Sohlenhaare = Plantar-bristles
dunkler Mittelbinde = median-stripe
Dornborsten = Spinous-bristles
Dornen = Spines
Wangenzahne = Cheek-teeth.
nadelförmig = Type 1. needle-like
spindelförmig = Type 2. spindle-shaped
spitzkeulig = Type 3. acutely clubbed
stumpfkeulig = Type 4. obtusely clavate
(The above four terms used in connection with the plantar bristles and the Ctenidia.)

GENERA AND GENERIC CHARACTERS OF THE GALEODIDAE

Roewer (1934, p. 505) has rightly remarked that this family is, in several characters—stigmatal combs, dentition, form of the flagellum, tarsal segments and haired claws, marked off from all other families of the solifugids and it is to be supposed that no worker who has been able to examine specimens from many areas would disagree with the view that it almost certainly contains many species and that, almost equally certainly some of these, are represented by several local races or subspecies. However, workers have always found difficulty in establishing morphological characters which might give a basis for an approximately accurate grouping into more or less natural genera, by which I understand characters, which, there is reason to suppose, have a longer phylogenetic history than those which we take to distinguish species. Roewer (*loc. cit.* pp. 505 and 506) gives a short history of these attempts and shows that up to the time at which he commenced his work on the group, four genera were accepted namely *Galeodes* Olivier 1791, *Paragaleodes* Kraepelin 1899, *Othoes* Hirst 1911 and *Galeodopsis* Birula 1903. In that same work however Roewer applied his system of the pattern of spinulation on tarsi II to IV to create seven new genera (added to later, (Roewer 1941,) by the acceptance of *Roeweriscus* Birula 1937). Few authors, apart from Birula have, since that time, been in a position to examine large numbers of species of this galeodid complex and although a few new species have been described since then and despite the fact that in the last decade the few workers on the group have been doubtful of the applicability of using a count of spines to distinguish the various genera,

nevertheless for want of a more firmly based system the new species have been fitted into Roewer's conspectus of the genera.

However, two facts would seem to make possible a new attempt at a solution to this problem even if, at the moment, it should be considered but tentative. Firstly Birula published in 1938 the volume on the solifugids in the series " Fauna SSSR " and although he is concerned only with those of that region he retains the genus *Paragaleodes* Krpln. despite the fact that it had been dropped from Roewer's system because the first tarsi were not without claws, although very rudimentary, in all its species and because its retention would have obviously cut across the system of classification which Roewer wished to introduce and which, it must be admitted, at that time seemed to make these multitudinous species more manageable and meaningful. The reason for which Roewer had rejected the genus *Paragaleodes* however dealt with only one of the characters which had been used to define it (see Kraepelin 1901) and Birula shows that it is possible to modify the original definition and to make a new and clearer diagnosis of the genus. However Birula's work seems not to have been consulted by later students, perhaps because it deals with a limited fauna not well represented in collections outside the U.S.S.R. (it was also written in Russian !) but also because the political conditions prevailing at the time of its publication prevented many of the greater libraries of the world from obtaining it. My own work on the collections from Israel, which are very rich in species of galeodids, convinces me that Birula and Kraepelin were correct in separating off this genus which seems to have a rather limited and continuous geographical range and which, as redefined by Birula, includes species which greatly resemble one another in their general fascies.

Another factor also, has operated to form my belief that it may now be possible to suggest a more natural grouping of the family Galeodidae. Panouse (*loc. cit.*) has rightly drawn attention to the fact that it will be extremely difficult to obtain a truly " natural " classification until we have knowledge of the post-embryonic development of these animals : at the moment almost nothing is known of this and neither will such knowledge be easily obtained. However during the course of my examination of the Israeli material I have been able to examine many immature forms—the detailed results of which will be communicated elsewhere—and one of the facts which has emerged seems to be of considerable importance for the present purpose of the generic division of the Galeodidae : this is, that the spinous or non-spinous condition of the distal segments of legs II to IV is much more stable than that of the proximal segments or even of the proximal pairs of spines on a single segment. It is noteworthy that even in 1941 Roewer published " intermediate formulae " for the spinulation of the second and third legs of *Galeodes* and that the differences there noticed (page 159) all refer to the proximal spines. A study of the immature stages of *Galeodes judaicus* (Kraepelin 1899) (=*Paragaleodes judaicus*) shows that the proximal spines may be acquired at different stages of development in different individuals. It seems obvious therefore that a system which bases its divisions on the presence or absence of a number of proximal spines will likely prove to be invalid. In the system of genera now proposed I have therefore taken into account the presence or absence of spines on the distal segments of

the tarsi only and where these could not be correlated with other characters I have considered it to mark the limits of subgenera ; as applied to the second and third tarsi this gives us a genus and a subgenus of quite limited and continuous geographical range viz. *Galeodopsis* and the subgenus *Galeodenna* (Roewer). I have disregarded the genus *Roeweriscus* since several species of the Galeodidae, not otherwise related, may show the development of similarly modified spines —placed it is true in varying positions—in connection with the flagellum-complex of the male, e.g. *Paragaleodes spinifer* Birula male. It is possible that when the males of more species are known and can be correlated with the relevant females we shall have a further reason for considering the differences in the various groups of setae of the chelae and their association with the flagellum.

KEY TO THE GENERA OF THE GALEODIDAE

1. Unguiculus more or less half the length of the pedunculus of the claw. *Othoes* Hirst 1911. (N.E. Africa)

1a. Unguiculus never more than one third the length of the pedunculus and usually only a quarter or less ..... 2.

2. The last tarsal segment of legs II and III with 2 spines : legs III and IV longer than the body in the adults of both sexes. Unguiculus a quarter to one third the length of the Pedunculus ..... *Galeodopsis* Birula

(Transcaucasia, Uzbekistan, Turkmenia and Eastern Iran.—It seems to be extremely doubtful whether *G. tripolitanus* Hirst 1912 belongs to this genus.)

2a. Last tarsal segment of legs II and III with 2 spines : only leg IV ever longer than the body. Unguiculus never more than a quarter of the length of the pedunculus ..... 3.

3. Pedipalpal metatarsus of more or less equal thickness throughout its length. Tarsus of pedipalp ovate. Tarsus I with a bush of hairs terminally and either without claws or with only rudimentary ones. Appendages short ; body, especially in the males covered with golden or bright canary yellow hairs. Male flagellum cochleariform, the two sides not symmetrically broadened ..... *Paragaleodes* Kraepelin 1899

(Extreme south-west of Asia, the Caspian sea area extending into central Asia as far as Turkestan, Arabia, northern Egypt and the northern coastal lands of Africa.)

3a. Pedipalpal metatarsus slimmer distally. Tarsus of pedipalp more or less pear-shaped. Tarsus I with a pair of small terminal claws usually easily seen. Appendages long. Body not covered with characteristic yellow hairs. Flagellum of male cultriform with the outline symmetrically broadened ..... *Galeodes* Olivier 1791.

(India, extending into central Asia west of the Altai and Tien Shan ranges to 50 deg. N. lat., all western Asia, Arabia and the whole of north Africa.) ..... 4.

4. (Sub-genera of *Galeodes*). With one or two spines on the last segment of tarsus IV ..... *Galeodellus* Roewer 1934

(India, Tibet, central Asia but not extending far to the east of the Tien Shan range, Iran Transjordan, Israel, Arabia and north Africa east of Morocco. The species from Arabia and north Africa, three only in number, tend to be abnormally spined at the geographical limits of the range. It includes the following " genera " of Roewer, *Galeodila*, *Galeodellus* and *Galeodarus*.)

4a. Last segment of tarsus IV without spines ..... 5.

5. With one spine on the last segment of tarsus III ..... *Galeodenna* Roewer 1934. (Deccan of India.)

5a. With two spines on the last segment of tarsus III ..... *Galeodes* sens. strict. (This includes the " genera " *Galeodibus*, *Galeodora* and *Galeodesus* of Roewer.)

SOME SPECIFIC CHARACTERS OF THE GALEODIDAE

Further research has added little to the characters available for the separation of species but it seems that two such may often be useful in helping to

distinguish the females of closely allied species and in correlating females with already known species where these have been diagnosed for the male sex alone. One of these characters is that of the number of teeth on the combs which overhang the opisthosomatal stigmata. Lawrence (1953) has used this in describing a species of *Galeodila* (=*Galeodellus*) and calls attention to the fact that they are more numerous in this species than for the genus *Galeodes* in so far as a specimen of the latter genus is figured by Roewer (1934, fig. 119). I find however that the variation in both the genus *Galeodes* and *Galeodellus* as well as other genera is very great and the range in each overlaps that in other genera. However, whilst it is a character of little use in distinguishing genera it can sometimes, even if but rarely, be used to differentiate between some of the seemingly closely related and very similar females of different species or even races of the same species such as undoubtedly occur in the widely ranging *Galeodes arabs* Koch 1842. As was to be expected, the number present varies from individual to individual but two closely related species were found to differ from a third undescribed species by the low and high counts respectively of these teeth, that is, two closely related species could not be distinguished by the sole use of this character but a third species, related to both, could be distinguished by a count of the spines. (This matter will be dealt with in more detail in my forthcoming monograph on the Israeli solifugid fauna). For this reason therefore I have added the number of teeth on the second opisthosomatal comb where they are usually better seen than on the first) to the descriptions of the species of this family described in the present paper.

Another character which can sometimes be used to distinguish species of Galeodidae is the form of the stridulatory setae in different species. I first discovered the use of this character when trying to distinguish between females of a new species of *Galeodes* and those of *G. arabs* Koch and *G. lacertosus* Roewer when the males of these three species could be shown to be distinct. For this purpose the character proved to be absolutely reliable and it was only after this experience that I discovered a paper by Birula (1925) in which he records the differences found in these setae in a comparison of *G. arabs* Koch and *G. araneoides* (Pallas). These two types of stridulatory setae (Figs. 1 and 2 are representative of them in the present paper) are undoubtedly basic types on which there has been superimposed, as it were, two or three further variations but one of the new species here described has produced a third main type (Fig. 4) which I have not encountered before and which may be of restricted range. As long ago as 1843 Hutton called attention to the fact that the only noise these animals make is a " hissing or whistling " sound and this must be produced by these special setae being rubbed against the opposite stridulatory plate. The exact function which this stridulation serves in the life of these animals is not completely clear but it is perhaps significant that the development of obviously different forms of the setae is most clearly manifested by nocturnal species such as are most of the Galeodidae : in families like the Rhagodidae, many species of which are apparently diurnal, no difference in these stridulatory spines as between species can be detected. These special spines are not always easily seen but may be discerned at once under the low power binocular microscope by turning the chela away from the observer and allowing the light to fall

on it from the front. Following Roewer's useful practice of numbering the ctenidial spines according to their type I propose to do the same for these stridulatory setae and shall at present recognize three such types :

1. " *Arabs*-type " i.e. those having the form of a fairly short very stout and highly chitinized basal rod, more or less rounded at the top, from which springs directly the thin flagellar portion.

2. " *Arancoides*-type " i.e. with the basal portion of the seta always thinner in proportion to its height than in type 1 and the top of this portion attenuated, usually on one side only, so that it merges gradually into the flagellar part.

3. " *Medusae*-type " (Fig. 4) i.e. with the basal part obviously thickened distally and partially truncate, the flagellar portion arising from one side of the truncated " head " giving the latter a shouldered appearance.

It is possible that each of these types will eventually be able to be separated into two sub-types according to whether they arise straight from the alveolus in which they are situate or whether, because the basal part of the spine is turned obliquely at the bottom, the whole spine is implanted at an angle. So far this latter condition has only been observed in the type II form although it may well be present in the others. Further work on this subject is desirable as indeed it may well prove to be on the whole of the chaetotaxy of the solifugid chela.

DESCRIPTIONS OF NEW SPECIES AND NEW RECORDS OF GALEODIDAE

GALEODES ANATOLIAE sp. n.

Holotype female captured by Dr Wahrman at Tuz Gölu, Turkey 2.viii. 1951. *Colour* : The chelae are mid-brown with two dark dorsal stripes ; the propeltidium is a lighter shade of the same colour with obscure darker markings and with very long setae which enclose a median lighter glabrous patch. The free tergites are violet-black contrasting somewhat with the opisthosomatal tergites which are a unicolorous dark sandy yellow with a violet-black stripe running the whole length. The legs and palpi are a light sandy yellow with the metatarsus of the palpi darker.

Spinulation : Tarsus IV. 2.2.2./2/0. Metatarus IV 1.2.2.; Tarsus III. 2.2.2/2. Metatarsus III. 1.2.2. Dorsally, at the commencement of the apical third of tibia IV is a very long seta reaching to the tip of tarsus IV ; in the basal third in another long seta reaching to the tip of the metatarsus. Metatarsus III with three dorsal spines ; Tibia III with one dorso-apical spine. Metatarsus II with five dorsal spines and one dorso-apical spine. Metatarsus of pedipalp with six pairs of ventral spines interspaced with six pairs of extremely long setae and arranged from the proximal to the distal ends of the metatarsus, *2.2.2.2.2.* 2.2.2.2.2.2.2. (where the *italicized* ones represent spines and the others setae). Chelae : moveable digit with two and the fixed digit with two intermediate teeth. Stridulatory setae of type II (supra), with the flagellar portion only about the same length as the basal portion. Tarsus I with two well developed claws. Ctenidia on the 6th sternite of the opisthosoma all of Roewer's Type 1. Stigmatal comb with 16 teeth either side, evenly graded, smallest laterally.

Measurements : Total length 27 mm. Length of propeltidium 7·0 mm. Breadth 5 mm. Length of chela 6·0 mm.

Pedipalp tarsus	2·5 mm.	Tarsus of leg IV	4·0 mm.	Tarsus of leg III	2·5 mm.
,, metatarsus	7·0 mm.	Metatarsus ,, ,,	7·5 mm.	Metatarsus,, ,,	5·5 mm.
,, tibia	8·5 mm.	Tibia ,, ,, ,,	8·0 mm.	Tibia ,, ,, ,,	5·0 mm.
,, femur	10·0 mm.	Femur ,, ,, ,,	8·0 mm.	Femur ,, ,, ,,	4·0 mm.

This species must be related to *G. clavatus* Roewer 1934 but differs in total size, the ventral spines of the third metatarsus and the general proportions. It is possibly related too to *G. roeweri* Kraus 1959 of which only the male is known but it appears to differ from this species also in total size, colour and the spines on metatarsus III.

Type : Zool. Mus., Hebrew Univ. of Jerusalem. SO. 147

GALEODES LYCAONIS sp. n.

Holotype female captured by Dr Wahrman at Aci Gölu 9. viii. 1951. *Colour*: Chelae a violet brown with two dorsal stripes, the sides light sandy yellow. Propeltidium light violet-brown anteriorly extending upwards and backwards in two patches either side of the middle line, posteriorly and at the sides light yellow. Free tergites and those of the opisthosoma dark sandy-yellow but the sternites and pleurites of the latter lighter. There is a dark median stripe which is much narrowed posteriorly but no dark side stripes on the sternites as in some other species. Legs, a lighter sandy yellow with the apical segments of all of them tending to be suffused with dark voilet. The pedipalp is yellow except for the tarsus, metatarsus, tibia and apical third of the femur which is violet-black. The malleoli are all a unicolorous light brown. Spinulation : Tarsus IV 2.2.2/2/0. Metatarsus IV ventrally spined 1.2.2.; tarsus III ventrally spined 1.2.2./2., metatarsus III ventrally 1.2.2. tarsus II ventrally 2.2.2/2. metatarsus II ventrally 1.2. Pedipalp ventrally with six pairs of spines, the tibia ventrally with seven pairs of spinous bristles. Metatarsus of leg III with three dorsal spines and that of leg II with five dorsal spines. Tibia of legs II and III each with one dorso-apical spine. Propeltidium with many very long setae, the anterior ocular hairs longer than the width of the ocular tubercle. The stridulatory setae on the chelae as Fig. 1. i.e. of type II and with the flagellum

Fig. 1.—*Galeodes lycaonis* sp. n. ♀. Stridulatory seta.

nearly twice as long as the base. Opisthosoma without ctenidial setae. Stigmatal comb with 12 large teeth either side, regularly but only slightly graded.

Measurements : Total length 30 mm. Length of propeltidium 6·0 mm. Breadth 9·0 mm. Length of chelae 6·5 mm.

Pedipalp tarsus	2·5 mm.	Tarsus of leg IV	4·0 mm.	Tarsus of leg III	3·5 mm.
,, metatarsus	9·0 mm.	Metatarsus ,, ,,	13·0 mm.	Metatarsus ,, ,,	6·0 mm.
,, tibia	11·0 mm.	Tibia ,, ,, ,,	11·0 mm.	Tibia ,, ,, ,,	8·0 mm.
,, femur	13·0 mm.	Femur ,, ,, ,,	11·0 mm.	Femur ,, ,, ,,	6·5 mm.

Moveable digit of the chela with three intermediate teeth and the fixed digit with two intermediate teeth but the right chela has a very small third intermediate tooth on the fixed digit, anteriorly : such abnormalities are not very rare in this genus. The systematic position which this species should occupy in the genus seems to be between *G. karunensis* Birula and *G. lapidosus* Roewer. If this is so it is of some interest to compare the geographical range of these two species, as far as it is known, with that of the species now described. Roewer (1934) says that Birula at first knew only of the females of *G. karunensis* which came from the Persian province of Arabistan and that subsequently other females and a male were obtained from the same place. Roewer then has a note which reads " Tiere beiderlei Geslechts, die mit dem untersuchten Typus ubereinstimmen, sahen wir aus Chusistan und Seistan." Chusistan (Khuzistan) is the more modern name of the old province of Arabistan and all the localities given for these two places lie in the Euphrates-Tigris plain and take in the salt desert land and dry water courses of the locality. Seistan is a large swamp area in eastern Iran near the borders of Afghanistan ; these two localities are some 900 miles apart but somewhat similiar in their ecological characteristics. *G. lapidosus* Roewer came from near Antaleya (=" Adalia ") on the gulf of Adalia in south Asia Minor, hot low coastal lands with dry river courses. The present species, *G. lycaonis*, like *G. anatoliae* previously described, come from the district of the great salt-water " lakes " on the central plateau of Asia Minor at an altitude of over 2,500 feet. Widely separated as these localities are there is a certain similarity in them which suggests that all three species may be ecologically modified elements of a former, larger and more widespread population.

Type. Zool. Mus., Hebrew Univ. Jerusalem. SO. 46.

GALEODES THEODORI sp. n.

Holotype male taken by Prof. Theodor at Qena, Egypt, 6. v. 1943..

Colour : Legs, pedipalps, chelae, propeltidium, free tergites and first two tergites of the opisthosoma a more or less murky olive-yellow. Rest of the opisthosoma is black whilst the malleoli are all smoke coloured. The hairs on the distal part of all the legs are a golden yellow whilst all the others are a dark brown.

Spinulation : Tarsus IV 2.2.2./2/0. Metatarsus IV 1.2.2. Tarsus III. 2.2.2./2. Metatarsus III, 1.2.2. Metatarsus II. 1.1.1.2.2. The unguiculus of all claws only about one eighth the length of the pedunculus. The pedipalpal metatarsus ventrally, is armed with six pairs of very short stout spines, with a pair of extremely long spinous bristles between each two pairs of spines. Around the mid-line of the pedipalpal metatarsus and through its whole length is a large number of cylindrical bristles. The tibia of the pedipalp bears, ventrally, only long spinous bristles and no spines. The ctenidial spines on tarsus IV are of Roewer's type 1 whilst those on sternite VI are of Type II.

The chelae (Fig. 3) are long and with three intermediate teeth on the movable digit and one on the fixed digit. The main tooth—the posterior one—on the movable digit is extremely large and well developed. Of the " cheek teeth ",

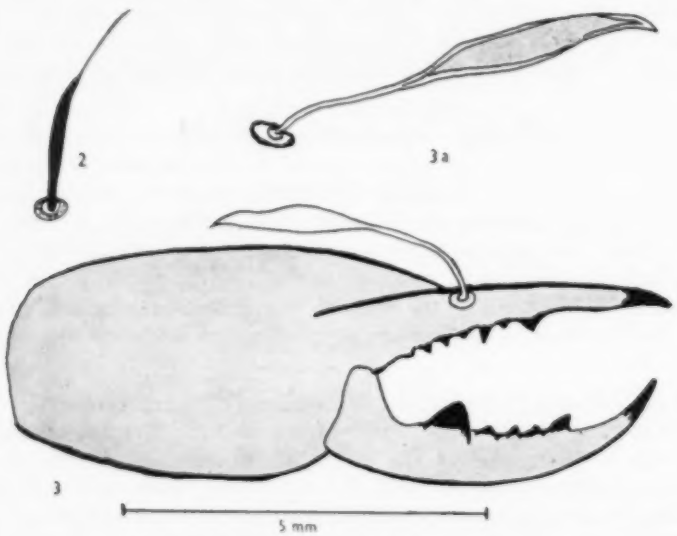
there are three lateral and two median. On the upper posterior angle of the stridulatory plate is a small bunch of light golden hairs and in front of the plate about 32 long, well chitinised stridulatory spines of type II (see Fig. 2) which have the flagellar portion short and stiff, and slightly angled with the basal portion. Stalk of chelal flagellum little longer than head. Leg I has very thin short claws, metatarsus of the pedipalp is thinned distally and the tarsus is pear-shaped, hence, despite the few golden yellow hairs on the legs there can be no doubt but that this species belongs to the genus *Galeodes*. Stigmatal comb with 15 very small, widely spaced teeth either side, each ending in a long seta 2/3 rds length of tooth.

Measurements : Total length 22mm. Length of propeltidium 4·5 mm. Breadth 5·0 mm. Length of chela 9·5 mm.

Pedipalp tarsus	1·5 mm.	Tarsus of leg IV	5·0 mm.	Tarsus of leg III	3·0 mm.
,, metatarsus	7·0 mm.	Metatarsus ,, ,,	7·5 mm.	Metatarsus ,, ,,	5·5 mm.
,, tibia	12·0 mm.	Tibia ,, ,, ,,	10·0 mm.	Tibia ,, ,, ,,	5·5 mm.
,, femur	8·5 mm.	Femur ,, ,, ,,	10·0 mm.	Femur ,, ,, ,,	6·0 mm.

So far as one may deduce from the already described males of species of *Galeodes* *G. theodori* is a very distinct form and would appear to have no very near relationships with other species.

Type : Zool. Mus., Hebrew Univ. Jerusalem. TH. 89.



Figs. 2.–3a—*Galeodes theodori* sp. n., ♂.
Fig. 2.—Stridulatory seta; Fig. 3.—Left chela viewed from inner surface.
Fig. 3a.—Flagellum more highly magnified. (×50.)

GALEODES MEDUSAE sp. n.

Holotype male taken by Professor Theodor at Qena, Egypt 6. v. 1943. (This specimen is abnormal in that the flagellum is only developed on the right

chela, the left one being in most respects similar to the condition as found in the females of *Galeodes*)

Colour : The whole animal is a dark brownish sandy colour and the hairs of the body and appendages are similarly coloured. The opisthosoma is similarly coloured with faint traces of a median stripe on the anterior tergites only. The tarsi of all the legs are a little darker than the other segments of these appendages.

Spinulation : Tarsus IV. 2.2.2./2./0., Metatarsus IV. 1.2.2. ventrally. Tarsus Tarsi IV with a dense covering, ventrally of type II ctenidia. III. 1.2.2./2. and metatarsus III. 1.2.2. ventrally. Dorsally, metatarsus III with three spines and tibia III with one dorso-apical spine ; metatarsus II with five spines and tibia II with one dorso-apical spine. Pedipalps with the metatarsus with eight to ten pairs of spines ventrally, some of those on the outer side being replaced by spinous bristles. Numerous cylindrical bristles are present. Tibia with six to seven pairs of lateral very stout and long spinous bristles and an irregular double median series of smaller and shorter ones. Chelae : these are in many ways very characteristic; the movable digit has two and the fixed digit has one intermediate teeth and there are three lateral and five median cheek-teeth. Anterior to the stridulatory plate are six to eight type II setae, thin and relatively weak and with the flagellum about twice as long as the base, dorsally to these are four to five type II setae which differ in being much stouter and in having the flagellum only about one third as long as the base. Enclosed in the angle made by these two types is a third type of stridulatory setae (type III supra) shown in Fig. 4. Of this type some 25 are present. In this type the flagellum is about one and a half times the length of the base. Opisthosoma VI. with a few type I ctenidia.

Measurements : Total length 52 mm. Length of propeltidium 10·5 mm. Breadth 13 mm. Length of chela 12·0 mm.

Pedipalpal tarsus	4·0 mm.	Tarsus of leg IV	11·0 mm.	Tarsus of leg III	5·0 mm.
,, metatarsus	20·0 mm.	Metatarsus ,, ,,	17·0 mm.	Metatarsus ,, ,,	13·0 mm.
,, tibia	30·0 mm.	Tibia ,, ,, ,,	22·0 mm.	Tibia ,, ,, ,,	17·0 mm.
,, femur	32·0 mm.	Femur ,, ,, ,,	25·0 mm.	Femur ,, ,, ,,	19·0 mm.

Fig. 4.—*Galeodes medusae* sp. n. ♂. Stridulatory seta.

The malleoli are exceptionally large, the 5th malleolus being 6·5 mm.
Type : Zool. Mus., Hebrew Univ. Jerusalem. TH. 90.

GALEODES (GALEODELLUS) PINKASI sp. n.

Holotype female taken by H. Pinkas at Mafrak, Transjordan in " Winter of 1948/1949."

Colour : Body dusky yellow-brown ; propeltidium lighter but with two violet patches anteriorly either side of the ocular tubercle. Chelicerae a darker

nut-brown with two faint darker dorsal stripes. Opisthosoma without a darker dorsal median stripe. Papli similar in colouring to the chelicerae but the tarsus, metatarsus and tibia infuscate. Legs all a light sandy yellow.

Spinulation : ventrally, Tarsus IV. 2.2.2./2./2. Metatarsus IV. 1.2.2. Tarsus III. 1.2.2.2./2. Metatarsus III 1.2.2. Sensory hair in the basal half of tibia IV reaching to half the length of the tarsus. Basal hair of tibia IV reaching to nearly half the length of metatarsus IV. Dorsally metatarsus III with three spines, tibia III with one dorso-apical spine : metatarsus II with five spines and tibia II with one dorso-apical spine. Pedipalpal metatarsus ventrally with six pairs of spines and with one pair of super-numerary ones between the basal pair. On the right palp only is another pair of these between the 2nd and 3rd pairs of spines and another lateral to the last and penultimate pairs. It is evident that there is a tendency here as elsewhere for the spinous bristles to be replaced by spines. In some species the reverse process occurs. Tibia of the pedipalp with a longitudinal row ventrally of five spines on the outer side only. Chelae. Movable digit with two intermediate teeth and the fixed digit with one intermediate tooth. There are four median and four lateral cheek teeth. Claws with the unguiculus one sixth the length of the pedunculus. The stridulatory setae are of type II but are modified in being bent at the base (Fig. 4a) and

Fig. 4a.—*Galeodes* (*Galeodellus*) *pinkasi* sp. n. ♀. Stridulatory seta.

with the flagellum about one and a half times as long as the base. Opisthosoma without ctenidia. Stigmatal comb with 26 teeth either side, scarcely graded and with irregularly spaced pairs of larger ones laterally.

Measurements : Total length 40·0 mm. Length of propeltidium 11·0 mm. breadth of propeltidium 6·5 mm. Length of the chela 15·0 mm.

Pedipalpal tarsus	3·0 mm.	Tarsus of leg IV	5·0 mm.	Tarsus of leg III	3·0 mm.
,, metatarsus	9·0 mm.	Metatarsus ,, ,,	10·5 mm.	Metatarsus ,, ,,	6·5 mm.
,, tibia	12·0 mm.	Tibia ,, ,, ,,	11·0 mm.	Tibia ,, ,, ,,	8·0 mm.
,, femur	12·5 mm.	Femur ,, ,, ,,	11·5 mm.	Femur ,, ,, ,,	10·0 mm.

This species is obviously near to *Galeodellus agilis* (Pocock) but is smaller than that species whilst the pedipalp is much longer. (Pocock gives the dimension of *G. agilis* pedipalp as 45·0 mm. whereas in the present species it is 65 mm.). Moreover Pocock (1895) says, in calling attention to the great length of the malleoli " The head of the 5th much longer than half the width of the carapace ". In the present species the 5th malleolus measure 3 mm. and the width of the propeltidium is 11·0 mm. The leg measurements given by that author are also very different but due allowance, in judging this character must be made for the fact that Pocock is describing a male. Even so there seems to be conclusive evidence that this is not the female of the Indian species described

by him. In many respects this species seems to me to show a connecting link between *Galeodila* and *Galeodellus* and undoubtedly *Galeodarus* is only a slightly specialized form of the first named group, hence I believe all three of these genera of Roewer's are best subsumed under one name and treated as one genus and since *Galeodellus* is the most widespread this name had best be selected for the designation of that genus.

Type : Zool. Mus., Hebrew Univ. Jerusalem. SO. 22.

GALEODES BICOLOR Roewer 1934

Collected by Dr Shulow in soft soil at Jerash, Transjordan, 18. xi. 1945. The type was taken from Mekran in Baluchistan (Prof. Roewer says Iran but this is in error, I think). The species proves to be fairly common and widespread in Israel. Adults seem to be taken later in the year than is usual for species of galeodids. Seemingly the males must be active for only a short time since it was unknown to Roewer and has not been indentified since. The stigmatal comb has 30 regularly graded teeth either side.

NOTES ON THE FAMILY SOLPUGIDAE WITH DESCRIPTIONS OF A NEW GENUS AND SPECIES

The family Solpugidae is perhaps more in need of the revision of its genera than any other family of solifugids and the difficulties attending this have been made sufficiently clear by Panouse (1950). Kraepelin (1901) divided the family into two genera viz. *Zeriassa* Pocock and *Solpuga* Lichtenstein em. Koch, Roewer (1934) accepted these two genera which he placed in the subfamily Solpuginae and to this subfamily he added some eighteen others, created by the application of his system of counting the tarsal spines. This, experience shows, more clearly perhaps here than in any other family, is untenable and, since it has not been possible during the last twenty-five years for any revision of the family to be undertaken authors have accepted this practice, making as necessary, new genera for any " abnormally " spined specimens which were discovered from time to time. Roewer had however made a great advance in dividing the family into two sub-families according to whether tarsus IV was six or seven segmented and this seems to me to be a valid division of great merit. At the present time it seems best for any worker on the group, in the absence of a detailed revision of even a section of the family, to make new genera only where a combination of characters clearly demarcates any species quite clearly from any other group of species, using for this purpose the male sex only and avoiding any great reliance on the spinulation of the tarsi. These principles have been applied in defining the new genus described in the present paper which seems to have affinites with genera as widely separated by Roewer's system as *Zeriassa*, *Solpugiba* and *Solpugelis*. This is not to say, however, that many of the characters used by Roewer for broadly grouping the genera, are inadmissable ; on the contrary, they seem likely to be the ones which will have to be utilized in making some division of the family when some students undertake its revision.

SOLPUGISTICELLA gen. n.

The dorsal plate of the rostrum bent sharply downwards as in the genus *Zeriassa* Pocock. Eye tubercle with one pair of long anterior setae and one shorter posterior pair (Fig. 5), otherwise glabrous. The metatarsus of legs II and III with a longitudinal row of five spines, all well developed and the pedipalpal metatarsus of the male without a scopula ventrally. On the fixed digit of the chela there is a small intermediate tooth standing in front of the anterior tooth. The male flagellum when recurved in its natural position does not extend further backwards than its base and the tip of the flagellum is characteristically branched. The ventral surface of the pedipalp with seven pairs of short, stout spines, the mid ventral surface with a large number of short, peg-like cylindrical-bristles. This genus is most closely related to *Zeriassa* Pocock although differing in the male secondary sexual characters and, incidentally, in the tarsal spinulation which for tarsus IV is 2/2/0/2/2/0 and for tarsi II and III, 2/0/0. Type species : *S. kenyae mihi.*

SOLPUGISTICELLA KENYAE sp. n.

Holotype male from Kenya, East Africa, probably Northern Turkana territory. No collector recorded.

Colour : Propeltidium a clear dark violet-black with a light yellow posterior border and a median yellow longitudinal stripe. The free tergites dusky. Opisthosoma with the sternites and pleurites all light sandy yellow, the tergites a light soft violet (except the last three which shade off to a light yellow) and each with a dark broad hind border. Eye tubercle black ; the chelae chestnut brown with two dorsal violet black stripes. Legs II to IV with the proximal segments, with the exception of the coxae, violet-black, the tarsi white. Leg I almost white. All coxae light yellow and the malleoli light yellow with a white border.

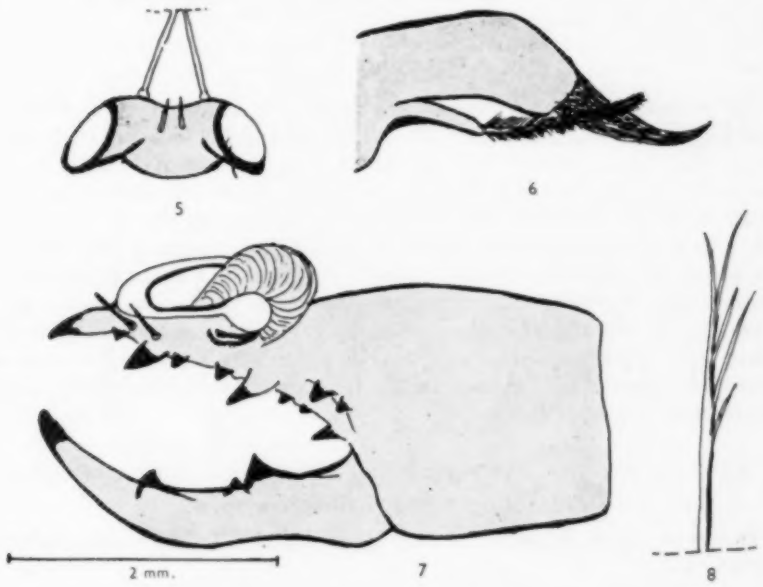
Spinulation : The ocular tubercle (Fig. 5) with one pair of long spinous-bristles and posterior to this two short seta. The anterior opisthosomal tergites with a pair of lateral spines each and between these a single unpaired very small spine, further posteriorly these spines gradually change into spinous-bristles. Leg IV. 2/2/0/2/2/0. Legs II and III, 2/0/0/. The metatarsus of legs II and III with a longitudinal row of five stout spines dorsally. Metatarsus of the pedipalp, ventrally, with seven pairs of short stout spines and the mid-ventral surface with many peg-like small cylindrical bristles. No accessory spines between the main spines on tarsi II to IV. Dorsal plate of the rostrum bent sharply downwards as in the genus *Zeriassa*, (Fig. 6). Chelae : These are of a very characteristic type and seem to separate off this new genus from the genus *Zeriassa*. On the moveable digit the anterior tooth is well developed but not in line with the other two teeth ; the intermediate tooth is separated from the anterior one by a fairly long intervening space and immediately posterior to it is the extremely large main-tooth. On the fixed digit the distal one of the two anterior teeth is very small—smaller than the second intermediate-tooth (they actually form a series of " one small, one large " repeated. There are two median and four lateral teeth representing the cheek-teeth. As will be seen from Fig. 7

the flagellum is equally characteristic ; just below the point of its recurvature are two stout spines, further forward than in *Zeriassa*, and below its point of origin two chitinous ridges which run together at the proximal end. The flagellum itself terminates in five seta-like branches (Fig. 8)—a form of flagellar ending not known in any other nearly related forms.

Measurements : Total length 11·0 mm. Length of propeltidium 3·0 mm., breadth 4·0 mm., length of chela, 4·0 mm.

Pedipalpal tarsus	7·5 mm.	Tarsus of leg IV	3·5 mm.	Tarsus of leg III	2·5 mm.
,, metatarsus	4·5 mm.	Metatarsus ,, ,,	4·5 mm.	Metatarsus ,, ,,	3·5 mm.
,, tibia	5·5 mm.	Tibia ,, ,, ,,	4·5 mm.	Tibia ,, ,, ,,	3·0 mm.
,, femur	5·5 mm.	Femur ,, ,, ,,	4·5 mm.	Femur ,, ,, ,,	2·5 mm.

Type : Zool. Mus., Hebrew Univ., Jerusalem. TH. 92.



Figs. 5–8.—*Solpugisticella kenyae* sp. n. ♂.
Fig. 5.—Ocular tubercle; Fig. 6.—Rostrum showing the declivity of the dorsal plate; Fig. 7.—Mesial surface of chela of male; Fig. 8.—Branches at the tip of the flagellum.

Besides the holotype male described above, the collection contains a female solpugid (No. Th. 93) which I believe to belong to the same species as the male but, since there are certain differences, some doubt remains as to the correct attribution of the specimen. I append a short diagnosis :—Female cf. *Solpugisticella kenyae mihi*, from Tseikuru, Kenya. January 1957. Total length ; 13·0 mm. *Colour* : Propeltidium and chelcerae, light yellow. Free tergites darker yellow. The opisthosomatal tergites, obscure olive horn-coloured, becoming darker posteriorly but the last tergite light yellow ; these tergites have two dark longitudinal bands running down them for the whole

length of the opisthosoma. All the sternites are light yellow and the malleoli white. The pedipalp is light-yellow with the exception of the tarsus and the distal part of the metatarsus which are a dark rust-yellow.

Spinulation : Tarsus IV. 2/2/0/2/1/0. Tarsus III. 2/1/0. This reduction by one spine on the 4th tarsus and the addition of one spine on the third tarsus is a deviation from the condition found in the male but it probably of no more significance than to confirm that a reliance on the tarsal spinulation, in any great detail, is almost certainly insufficient for separating species and certainly so for separating genera. The ventral surface of the pedipalpal metatarsus with four pairs of spinous-bristles and a single unpaired spinous-bristle almost at the junction with the tibia. Chelae : the dentition of these is more or less the same as in the male except that there are three median-teeth the hindermost one being extremely small and apart from this all the cheek-teeth are arranged as in the male described above.

SOLPUGA sp.

The present collection contains three tubes of immature forms and a female of some species of this genus (Ref. No. SO. 55, 56 and 58) collected from Jerash, Transjordan, 18 xi. 1945. I do not think that the material can be further identified with any certainty but the record is important since it gives yet further evidence of the existence of this predominantly Ethiopian family in Asia, a fact to which I called attention in a former paper (Turk 1948). In that paper too I recorded a specimen from Gaza as " ? *Solpugella asiatica* Roewer 1934 " but I now think that this specimen was, in fact, not a female of that species but a teratological (partially gynandromorphic) example of the present species of *Solpuga* even although there were some slight variations in the spinulation of the tarsi—a condition which is found, even within species, very frequently in this family.

NEW RECORDS AND DESCRIPTIONS OF NEW SPECIES OF RHAGODIDAE

RHAGODIXA TRANSJORDANIA sp. n.

Holotype female collected by H. Pinkas, Mafrak, Transjordania, in Winter of 1948/1949.

Colour : Chelae black ; the propeltidium shining black with a narrow, anterior white border. Free tergites black and the whole dorsum of the opisthosoma black. Ventrally the chelae are pale orange colour as are all the coxae ; the sternal scuta, all a dusky grey except the last two which are black. All the body hairs a dark chocolate brown. Legs II to IV a bright orange colour ; Legs I, black ; tarsus and metatarsus of the pedipalp black. All hairs and spines a dark red-brown. Setae at the extreme tip of the tarsus of the pedipalp and Leg I, malleoli all light yellow. The colour pattern makes this a very striking and unusually beautiful form.

Spinulation : Tarsus II and III ventrally, 1.2. Tarsus IV 2.2.2. Metatarsus III ventrally, 2.2. Metatarsus IV. 1.2.2. Dorsally the spinulation of the legs is :— Metatarsus III with six spines (four dorsal and two dorso-lateral) metatarsus II

with six dorso-lateral spines. Tibia III with three dorso-apical spines and tibia II with one dorso-apical spine. The eyes are placed on top of the ocular tubercle and point directly upwards. On coxae I to III are eight to twelve bacilli which gradually increase on the posterior coxae but as in most rhagodids they are not in equal number on the right and left sides of the animal. Chela (Fig. 9) powerfully toothed and the fixed digit with two anterior-teeth and one very large main tooth. Of the cheek-teeth there are five lateral and two median. The stridulatory plate has six main ridges with smaller and much weaker ones at either end. There are about a dozen very short and weak stridulatory setae in a row immediately in front of the plate, in the anterior concavity and about 20 longer and stronger ones in irregular rows in front of these.

Measurements : Total length 43 mm., Chelicerae 11 mm. long. Propeltidium 5 mm. long and 6 mm. broad. Pedipalpi: Tarsus 0·75 mm., metatarsus 3·5 mm. tibia 6 mm. Although the tarsal spinulation, according to Roewer's system quite clearly indicates this genus nevertheless the size and the colour pattern of the animal quite clearly indicate its relationship to the species comprised in the genus *Rhagodia* Roewer 1933. When a revision of this family is eventually undertaken this species will no doubt find its place among the species of the latter genus.

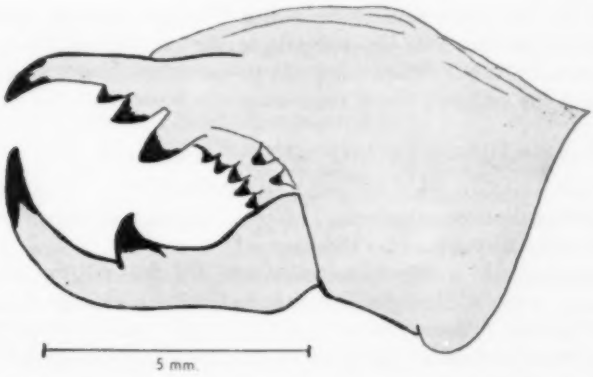


Fig. 9.—*Rhagodixa transjordania* sp. n. Chela of female.

Type : Zool. Mus., Hebrew Univ. Jerusalem SO. 23.

NEW RECORDS OF A SPECIES OF KARSCHIIDAE

GYLIPPUS sp.

An immature stage of some species of this genus was taken from the island of Socotra in Dec. 1942. The species differs in its dentition from either *G. syriacus* Simon 1872 or *G. quaestiunculus* Karsch 1880 and is almost certainly a new species. This is an important record since the genus is not otherwise known south of Mesopotamia, indeed the only solifugid of this family that appears to be recorded from Socotra is the "*Gluviopsis balfouri*" of Pocock which is doubtfully placed in that genus.

NEW RECORDS AND DESCRIPTIONS OF NEW SPECIES OF DAESIIDAE

Subfamily Gluviopsinae

GLUVIOPSIS PAPHLAGONIAE sp. n.

Holotype female collected by Dr J. Wahrman at Eregli, Turkey 6. viii. 1951.

Colour : Chelae, propeltidium and 1st legs a dark rust brown. Opisthosoma a light yellow and all the malleoli a lighter shade of yellow. Pedipalpi, light yellow except the tarsus, metatarsus and femoro-tibial joint, all of which are a dark violet black.

Spinulation : Tarsus IV, three-segmented and spined 2.2/2/2.2.2. Tarsus III one-segmented and spined 1.1.2.2.2. Metatarsus III, ventrally spined 2.2.2 and dorsally 1.1.1. The spinous-bristles of the pedipalps are arranged as follows : Tarsus with one ventral median one. Metatarsus ventrally with 2.2.2.2.2.2. Tibia ventrally with 2.2.2.2.2.2. (these are all true spinous-bristles and not spines as in other species of the genus) the femur spined 2.2. ventrally. Measurements : Total length 9 mm. Propeltidium ; total length 1·5 mm. and breadth 1·75 mm. Length of chela 2·75 mm.

Pedipalpal tarsus	0·3 mm.	Tarsus of leg IV	0·6 mm.	Tarsus of leg III	0·5 mm.
,, metatarsus	1·8 mm.	Metatarsus ,, ,,	1·8 mm.	Metatarsus ,, ,,	1·0 mm.
,, tibia	2·0 mm.	Tibia ,, ,, ,,	2·2 mm.	Tibia ,, ,, ,,	1·25 mm.
,, femur	2·0 mm.	Femur ,, ,, ,,	2·1 mm.	Femur ,, ,, ,,	1·2 mm.

This species obviously has relationships with *G. atrata* (Pocock) both by colour and the ratio of the length of the pedipalp to the breadth of the propeltidium (vide Kraepelin 1901) but differs markedly in the spinulation and in the length of the tibia of the pedipalp being more than the breadth of the propeltidium.

Type : Zool. Mus., Hebrew Univ. Jerusalem SO. 45.

GLUVIOPSONA NOVA sp. n.

Holotype female taken above the Temple of Artemis, Jerash, Transjordania. 15. xi. 1945 (no collector's name given).

Colour : Propeltidium, a light chesnut-brown, the free tergites and the opisthosomal tergites violet-black ; pleurites and sternites a whitish or sandy yellow. Chelae, dark brown. All legs and palpi a light sandy yellow except the metatarsus and the femoro-tibial articulation of the last which is a pale violet-black. Malleoli all whitish-yellow.

Spinulation : Tarsus IV, 3-segmented, tarsi II and III, 1-segmented the spinulation of tarsus IV being 1.2./2./2.2. and that of tarsus II and III being 1.2.2.2.2. The chelae exactly as figured by Roewer 1934 for *Gluviopsona persica* (Birula 1904) male. Tarsus of pedipalp (Fig. 10) with one unpaired ventro-median spine ; the metatarsus with six pairs of weak spines ventrally and the distal half of the tibia with four pairs ; the femur of the pedipalp with four ventro-lateral apical spines each side but these are irregularly arranged and not in pairs, 2.2.—a somewhat peculiar feature : it is indeed doubtful whether all these structures should be classed as spines and not spinous-bristles since they are almost a transitional stage between the two. The metatarsus of the pedipalp has, in addition, a few short, sparse cylindrical bristles. Opisthosoma without ctenidia.

Measurements : Total length, 11·0 mm. Propeltidium, length 1·7 mm. breadth 2·0 mm. length of chela, 3·0 mm.

pedipalp	Tarsus	·75 mm.	Tarsus of leg IV	1·3 mm.	Tarsus of leg III	·8 mm.
,,	metatarsus	2·5 mm.	Metatarsus ,, ,,	2·2 mm.	Metatarsus ,, ,,	1·2 mm.
,,	tibia	3·0 mm.	Tibia ,, ,, ,,	3·0 mm.	Tibia ,, ,, ,,	2·2 mm.
,,	femur	3·0 mm.	Femur ,, ,, ,,	3·5 mm.	Femur ,, ,, ,,	2·0 mm.

It might be thought that this was the hitherto unknown female of *G. persica* (Birula), a species of which only the male sex is known, but it differs from that species, despite the identical form of the chelae, in having only six pairs of spines on the pedipalpal metatarsus and four on the pedipalpal tibia whilst the ventro-lateral arrangement of the spinous-bristles on the femur is quite different from anything found in the male of that species. There are some differences also in the colouring of the opisthosoma and in the spinulation of tarsus IV.

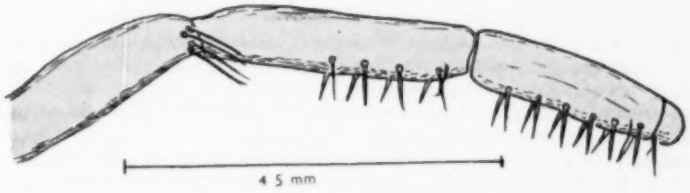


Fig. 10.—*Gluviopsona nova* sp. n. ♀ Pedipalp showing spinulation and the characteristic arrangement of spinous-bristles on the pedipalp.

Type : Zool. Mus., Hebrew Univ. Jerusalem SO. 59.

NEW RECORDS OF A SPECIES OF AMMOTRECHIDAE

Hemerotrecha cf. *californica* (Banks 1899), Muma (1951) by a study of several male specimens has been able to divide this complex of closely related species into several distinct species, although, as he himself admits, some of these may be of doubtful validity. Muma calls this group of species the " *banksi* group " and it is certain that the single female in the Hebrew University's collections belongs to it. This individual is damaged and may be immature but the genital operculum, as far as it can be made out from the specimen, seems to agree most closely with *H. californica*. The locality data are given simply as " Contra Costa, California ".

SUMMARY

In the introduction to this paper the characters at present used in the study of the systematics of the solifuga are discussed. The characters used to divide the genera in the family Galeodidae are dealt with in more detail and a new system of division for the family is proposed followed by a key to the genera and subgenera which at present it seems best to recognize. Some of the genera erected by Roewer are reduced to subgenera and others are made synonyms of those recognized in the key. On the basis of previous work by Birula, three types of stridulatory setae are proposed for recognition with suggested sub-types the use of these in distinguishing between closely related females is discussed

and their general use as specific characters is shown to be possible. The use of the varying number of teeth on the stigmatal combs is mentioned as a specific character which it is possible to use in a limited number of instances. The following species are described as new to science :—*Galeodes anatoliae*, *G. lycaonis*, *G. theodori*, *G. medusae*, *G.* (*Galeodellus*) *pinkasi*, *Solpugisticella kenyae* gen. et sp. n., *Rhagodixa transjordania*, *Gluviopsis paphlagoniae*, *Gluviopsona nova*. A species, probably new, of *Gylippus* is recorded from the island of Socotra (the first record of the genus from this part of the world). A *Solpuga* sp. is recorded from Transjordan adding yet another species to the growing number of extra-ethiopian forms in the family ; the "*Solpugella asiatica* Roewer" recorded by the author in 1948 is now thought to be an individual of this same *Solpuga* sp. A specimen referred to the "Banksi"-group of the genus *Hemerotrecha* is recorded from Contra-Costa, California.

REFERENCES

Birula, A. A. (1925). A Note on some differential characters between *Galeodes arabs* C. Koch and some allied species. *Ann. Mag. nat. Hist.* (9) **15** : 192-200.

Birula, A. A. (1938). Solifuga : Arachnides. *Fauna SSSR.* **1** No. 3.

Hutton, T. (1843). Observations on the habits of a large species of *Galeodes* (*vorax*). *Ann. Mag. nat. Hist.* **12** : 81.

Kraepelin, K. (1901). Arachnoidea : Palpigradi und Solifugae. *Das Tierreich* **12** : 4-159.

Lawrence, R. F. (1953). A collection of African Solifugae in the British Museum. *Proc. zool. Soc. Lond.* **122** : 955-972.

Muma, M. H. (1951). The arachnid Order Solifugida in the United States. *Bull. Amer. Mus. nat. Hist.* **97** : 35-141.

Panouse, J. B. (1950). Sur la systematique des Solifuges. *Bull. Mus. Hist. nat., Paris* (2) **22** : 717-722.

Pocock, R. I. (1895). On the species of Galeodidae inhabiting India and Ceylon. *J. Bombay nat. Hist. Soc.* **9** : 438-452.

Roewer, C. F. (1932-1934). Solifugae, Palpigradi. in *Bronn's Klassen und Ordnungen des Tierreichs.* **5**, Abt. 4. Buch 4. 1-723.

Roewer, C. F. (1941). Solifugen 1934-1940. *Veröff. deutschen Kolon.-u Uebersee-Mus.* **3** : 97-192.

Turk, F. A. (1947). On two new species of the family Galeodidae (Solifuga) from Asia. *Ann. Mag. nat. Hist.* (11) **14** : 74-80.

Turk, F. A. (1948). On recent additions to the collection of Solifuga belonging to the Hebrew University of Palestine. *Ann. Mag. nat. Hist.* (12) **1** : 263-273.

Writtick, R. J. (1939). Notes on Solifugae (Arachnida), I. Galeodidae. *Ann. Mag. nat. Hist.* (11) **4** : 444-450.

FURTHER OBSERVATIONS ON THE COMPARATIVE ANATOMY OF THE HEAD IN THE NEMATODE FAMILY SUBULURIDAE : WITH THE DESCRIPTION OF A NEW SPECIES

BY

WILLIAM G. INGLIS, B.Sc., Ph.D.

Department of Zoology, British Museum (Natural History)

[Accepted 9th February 1960]

(With 8 figures in the text)

A new species of the genus *Subulura* is described from the (?) caecum of *Rhabdomys pumilio* (type host) and *Rattus* (*Praomys*) *namaquensis* at Cape Province, Union of South Africa. The species is charcterized by the presence of six lip-lobes and by equal spicules with barbs on their posterior ends. The structure of the head in the family Subuluridae is analyzed and it is argued that lobed mouth openings have appeared, separately, four times and that the development of the lobes has been to improve the efficiency of the mouth as a gripping organ. It is suggested that, associated with the appearance of a more " open " mouth the pharyngeal portions have been modified as triturating organs. It is pointed out that this hypothesis is opposed to the interpretation of the structure of the head, in the family Subuluridae, put forward by Chitwood and Chitwood. *Subulura indica* Khera, 1956 is considered a synonym of *Tarsubulura perarmata* (Ratzel, 1868) and *Subulura vulpis* Khera 1956 a synonym of *Oxynema alata* (Mazhar, 1933). *Subulura armata* Vuylsteke, 1957 is referred to the genus *Allodapa*. The subfamily *Leipoaneminae* Chabaud, 1957 is accepted for the genus *Leipoanema* Johnston and Mawson, 1942.

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INTRODUCTION

Recently I (Inglis, 1958) suggested that three trends of morphological modification could be demonstrated in the head within the family Subuluridae. All the trends were considered to lead from a simple, unlobed hexagonal mouth opening to a complex mouth opening bounded by lip-lobes. However the modification was demonstrated in detail along only two of the lines, from a hexagonal to a triangular mouth opening in the subfamily Parasubulurinae and from a simple hexagonal to a lobed-hexagonal mouth opening in the subfamily Allodapinae. In the subfamily Subulurinae only two head forms were described, a simple hexagonal mouth opening in *Subulura* and *Oxynema* and a complex twelve-lobed mouth opening in *Labiobulura*. No forms intermediate between the two mouth forms were described. It is now possible owing to the

kindness of Dr R. J. Ortlepp and Dr P. Mawson to supply the " missing links " in this subfamily. The former sent me specimens of a nematode, referable to the subfamily Subulurinae, which has a mouth-opening intermediate in form between the simple *Subulura-Oxynema* type and the complex *Labiobulura* type and the latter has sent me a description of the head of *Labiobulura peragale* which confirms the original description. The specimens from Dr Ortlepp appear to represent a new species which is here named *Subulura ortleppi*.

SUBULURA ORTLEPPI sp. n.

Type Host : *Rhabdomys pumilio* (Sparrman, 1784), (?) caecum. Cape Province, Union of South Africa, 9♂♂, 6♀♀ of which 1♂ is here selected as Lectotype.

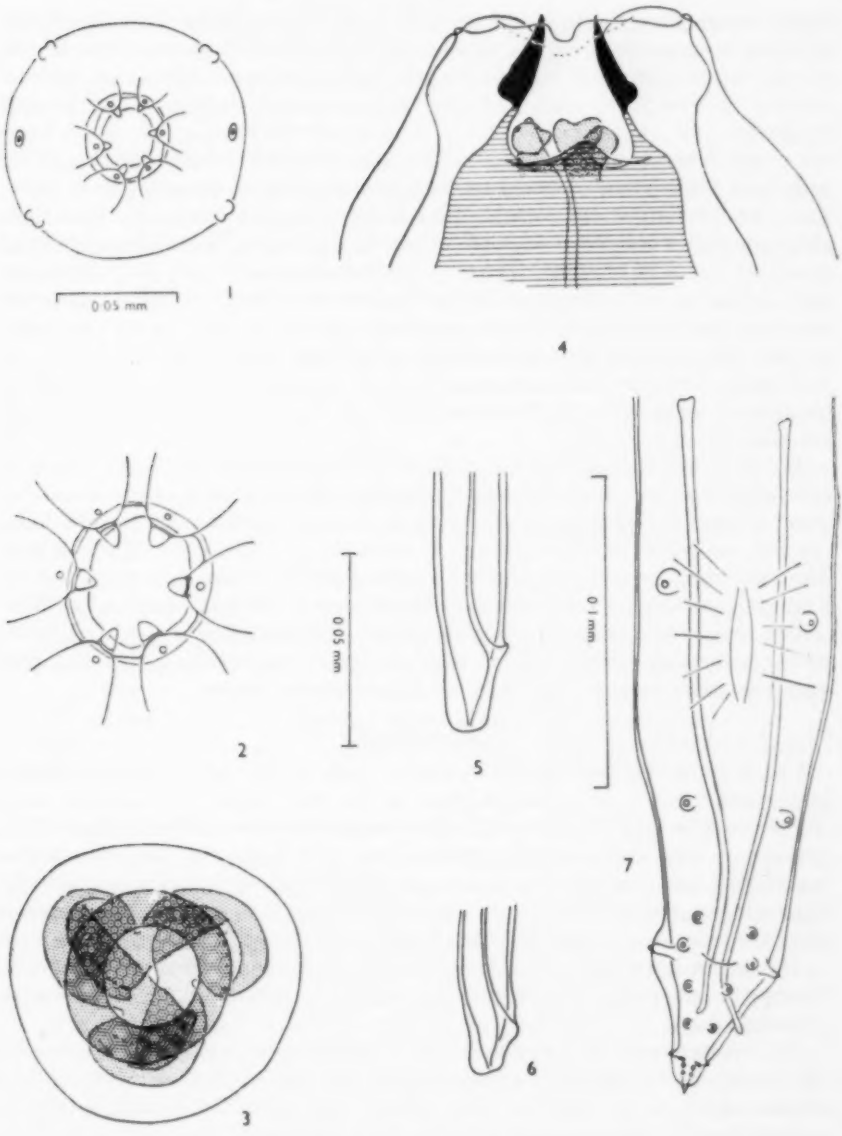
Other Host : *Rattus* (*Praomys*) *namaquensis* (A. Smith, 1834), (?) caecum. Cape Province, Union of South Africa.

The male is 11-13 mm. long, the oesophagus is 1·35-1·47 mm., the spicules are equal, 1·1-1·4 mm. and the tail is 0·25-0·30 mm. The female is 24-27 mm. long, the oesophagus is 1·65-1·83 mm., the tail is 1·45-1·60 mm. and the vulva is 9·0-10·5 mm. from the anterior end of the body.

Morphology of the head.

The mouth opening is complex hexagonal, bounded by six lip-lobes in a way exactly comparable to that found in the *Allodapa baylisi* group (Inglis, 1958 Fig. 3 ; Fig. 1 in the present paper). The head carries the four double papillae in an external circle and the inner circle of six single papillae characteristic of the family. The papillae of the inner circle are borne on the lip-lobes at their ends nearer the centre of the head (Figs. 1 & 2). The buccal cavity is circular in cross section and is divided anteriorly into six narrow pointed projections, one of which corresponds to each lip-lobe. The specimens of this species are in very good condition so that it is possible to study the head in greater detail than was possible with any of my specimens of the *Allodapa baylisi* group and certain points of interest are now apparent. Thus, at first glance the buccal cavity appears to be hexagonal in cross-section, but this is an effect produced by the flexure of the anterior prolongations of the lining of the buccal cavity. Behind this level the buccal cavity is circular ; further, the hexagonal appearance is restricted to the inner lining of the anterior part of the cavity and does not affect the outer side of its wall (see Fig. 2). More posteriorly the wall of the buccal cavity has an undisturbed circular section (Fig. 3). This internal distortion of the buccal cavity anteriorly is only to be expected when a flexible structure, or series of structures, originates from a circular source. When the anterior prolongations bend inwards from the straight antero-posterior arrangement of the buccal cavity, even although they have narrowed, some distortion of the basic circular arrangement must occur, leading to a hexagonal appearance.

So far the head is exactly the same as that found in *Allodapa baylisi* but the arrangement of the pharyngeal portions is different and corresponds to the lobed and helically arranged condition diagnostic of the subfamily Subulurinae. The pharynx is cupped anteriorly, with the outer limits of the cup determined by three anteriorly directed parts of the oesophagus which are fully embedded



Figs. 1–7. *Subulura ortleppi* sp. n.

1. *En face* view of whole head. **2.** *En face* view of mouth opening showing detail of the anterior ends of the prolongations from the lining of the buccal cavity, the distribution of the inner papillae and the apparent hexagonal form of the buccal capsule. **3.** *En face* view of the pharyngeal portions showing their helical arrangement and the circular outline of the buccal capsule. **4.** Dorsal view of head. **5 & 6.** Details of posterior ends of two spicules. **7.** Ventral view of male tail showing distribution of the caudal papillae. (Figs. 1 & 4 ; 2, 3, 5 & 6 to the same scale.)

in the surrounding tissue of the head (Fig. 4). These three structures, each of which corresponds to and is continuous with one of the three sectors of the tri-radiate oesophagus, are called the *pharyngeal portions*. Within the cupped anterior end are three pairs of further lobes, one pair corresponding to each peripheral lobe : three *radial lobes* and three *chordal lobes*. The radial lobes are wedge-shaped when viewed *en face* with their points towards the axis of the body and their bases attached to the inner surfaces of the peripheral lobes. They are not fully distinguishable from the peripheral lobes in this head form although they are distinct in some others in the family (e.g. *Labiobulura* and *Hapalulura*). The chordal lobes also originate at the base of the pharyngeal-cup, alongside the corresponding radial lobes but they extend in an anti-clockwise direction to over-lie the neighbouring portions to produce the spiral or helical appearance so characteristic of this type of head (Fig. 3).

Prominent cervical alae are present which broaden suddenly just posterior to the head and narrow rapidly again about the level of the posterior end of the oesophagus.

The male tail is typical of the subfamily Subulurinae (Fig. 7). There is an elongate precloacal sucker without cuticular elaborations and the usual ten pairs of caudal papillae, the arrangement of which is shown in figure 7. The spicules are equal in length, identical in structure and highly characteristic. They are blunt posteriorly and carry marked barbs on one side (Figs. 5 & 6). The tail is relatively short posterior to the most posterior pair of caudal papillae.

The female is typical of the subfamily. The vulva is about the middle of the body and opens into the usual complex ovojectoral apparatus. The eggs are embryonate *in utero* and the tail is evenly pointed.

DISCUSSION

I have given this species a new name in spite of the thirty names of species inquirenda listed in my previous paper on the subulurids. No head structure similar to that described above has been reported before and the shape of the spicules is very characteristic, their square ends being obvious even at low magnifications. In spite of our lack of detailed knowledge of host-specificity in nematodes, the fact that no member of this family has hitherto been reported from the same hosts adds provisional support to the policy adopted.

The name is chosen not only because I received the specimens from Dr Ortlepp but also as a recognition of the contributions he has made to systematic nematodology.

The species is referred to the genus *Subulura* Molin, 1860 since it possesses the buccal cavity, circular in cross section, and the lobed pharyngeal portions characteristic of that genus. The form of the mouth, with six lip-lobes, is not typical of the other species of the genus but I prefer, as with the corresponding *Allodapa baylisi* group, not to introduce a new genus for it but to refer it to the genus *Subulura* until a fuller revision of the subulurids can be undertaken. The diagnosis of the genus *Subulura* must, therefore, be expanded to accept *S. ortleppi*, thus :

> Subulurinae : mouth opening basically hexagonal, simple or complex ; when complex anterior prolongations of the buccal cavity lining narrower

than the lip-lobes ; peripheral lobes of pharyngeal portions wholly muscular ; cervical alae present. Male : pre-cloacal sucker without any cuticular elaborations ; both spicules fully cuticularized.

Type Species : *Subulura acutissima* Molin, 1860.

THE STRUCTURE OF THE HEAD OF *LABIOBULURA PERAGALE*

Dr P. M. Mawson has informed me by letter, that the mouth opening in *Labiobulura peragale* (Johnston and Mawson, 1940) is in fact bounded by only six lip-lobes as stated in the original description and not by six lip-lobes and six inter-labial lobes as I suggested might be the condition (Inglis, 1958 p. 595). She further informs me that the buccal cavity is circular in cross section, and the pharyngeal portions are very similar to those found in *L. peramelis*, that is the peripheral lobes are fully cuticular and the radial and chordal lobes are free standing. The importance of this information will become clear later but it may be pointed out here that this head form supplies another ' missing link ', in this case between that characteristic of *S. ortleppi* (Fig. 8 b) and the extremely complex form found in *L. peramelis* (d.). I do not consider it necessary to recognise the different head form in *L. peragale* systematically above the species level and it is left in the genus *Labiobulura* which is now re-diagnozed, thus :

Subuluridae : mouth opening basically hexagonal, complex, with six lip-lobes with which there may be six triangular inter-labial lobes ; peripheral lobes of pharyngeal portions wholly cuticular ; radial and chordal lobes standing erect and free within the cup formed by the peripheral lobes, slightly muscular ; no cervical alae. Male : pre-cloacal sucker elongate, without cuticular elaborations ; spicules both fully cuticular.

Type Species : *Labiobulura peramelis* (Baylis, 1930) Skrjabin and Schikhobalova, 1948.

TRENDS IN THE MORPHOLOGY OF THE HEAD IN THE SUBULURIDAE*.

It is now possible to demonstrate three complete lines of morphological modification, all of which start from a simple hexagonal mouth opening and culminate in complex, lobed mouth openings. In two of the lines, associated with the change in the form of the mouth opening, the pharyngeal portions alter from fully muscular to fully cuticular. These lines are recognized systematically as the subfamilies Subulurinae and Parasubulurinae. This change in the structure of the pharyngeal portions is not found in the third line of modification, the subfamily Allodapinae, but this is not surprising since it would be morphologically very difficult for such a change to be apparent in the pharyngeal portions characteristic of this subfamily. That is, portions which bear a series of ridges on their inner surfaces ; the possibilities for change in animals always being restricted by the complexity and form of the existing structures. These three lines of modification are represented diagramatically in Fig. 8, in which

*In my previous paper I refer to the family Subuluridae Yorke and Maplestone, 1926 and to the subfamily Parasubulurinae López-Neyra, 1945. This is incorrect : the family name should be attributed to Travassos, 1914 and the subfamily name to Berghe and Vuylsteke, 1938 since they first recognized taxa within the family group with *Subulura* and *Parasubulura* as type genera.

the parallel trends in the increasing complexity of the mouth openings are shown vertically while the close correspondence of the three lines at all stages is shown horizontally. The degree of parallelism is very high, particularly between the Subulurinae and the Allodapinae. Note particularly the virtual identity of the external form of " b " and " k ", which are totally distinct internally. In the diagram the words ' muscular ' and ' cuticular ' at the left-hand side indicate the form of the pharyngeal portions corresponding to the various mouth forms included in the first two columns.

Feeding in the nematoda is based on the principle of the pump, food particles, or fluid, are sucked into the gut. Such a method has certain inherent disadvantages : (1) the food particles must be small enough to pass down the lumen of the oesophagus or the food must always be in the form of a fluid. The importance of the maximum size of the particle must be relatively critical since the structure of the oesophagus, with its system of radial muscles, will not allow it to stretch beyond a fixed limit. (2) The method must be inefficient if the food particles cannot be brought, by some mechanism or other, close to the anterior end of the digestive tract. The ' anterior end ' for this purpose not necessarily being the mouth opening but the point at which the lumen of the digestive tract is complete—that is fully enclosed. Thus the ' anterior end ' in the Subuluridae must be considered, functionally, as shifting posteriorly as the elaboration of the lip-lobes produces a more open mouth. When particulate food is taken the two limiting factors set out above become important and it appears that the various head forms within the subulurids have been developed to overcome them. Clearly the development of some form of jaw or holding structure or structures, will be of great advantage and this, I suggest, is the functional explanation of the various modifications of the mouth opening in the subulurids. That the advantages to be gained are great is amply confirmed by the way in which the same type of modification has occurred along three independent lines of modification. Further evidence in support of the contention that the mouth opening is modified to bring food nearer the effective anterior end of the gut is available in the tendency for the pharyngeal portions to become more cuticular in those forms with the most highly modified, and more open, mouth openings.

A simple end to the lining of the buccal cavity, as in head forms " a," " e." and " j," (Fig. 8) must be able to do little more than strengthen the anterior end of the head, and the mouth opening, and can be of little use in the actual trapping or holding of food particles. Such a mouth must be relatively inefficient unless, or until, it is closely apposed to the food particle. In the " b " and " k " forms the development of pointed processes on the anterior edge of the lining of the buccal cavity will produce a mechanism which can, at least, hold food particles in position against the mouth opening. This introduces a complication, such processes must be able to move and I interpret the lobing of the mouth opening as having developed to allow this to happen. The lobing of the " b " and " k " mouth forms is mainly due to the development of bumps on the anterior surface of the head, one corresponding to each process from the lining of the buccal cavity, the mouth opening still remaining, fundamentally, simply hexagonal bounded by the lobes which are free from

each other at their extreme inner ends nearer the centre of the mouth only (Fig. 2), being fully joined together more radially. In the mouth openings " c " and " d ", however, the lip-lobes are fully free from each other and can bend freely about their lines of attachment to the remainder of the head. The mouth opening has as a result become effectively larger, so that larger particles of food can pass into the buccal cavity. With this change is associated the appearance of fully cuticular pharyngeal portions, (also in " i " but this is considered later), which may be considered as acting as a triturating mechanism. Head form " b " can still only accept particles over a limited range of size while the form " c " and " d " can accept much larger particles which must introduce a complication due to the limit imposed by the size of the lumen of the oesophagus.* Some mechanism appears to be necessary to compensate for this and I suggest that the pharyngeal portions now act as a mechanism for reducing the size of the food particles to a point where they can pass easily along the lumen of the oesophagus. There has as a result been a tendency for a posterior shift in the effective anterior end of the oesophagus, from the mouth opening in the " a " and " b " forms to the posterior end of the pharyngeal portions in the " c " and " d " forms. Associated with this is a change in the functions of the lip-lobes between " b " and " c ". In " b " their sole purpose it to hold food particles while in the " c " and " d " forms they have the additional function of passing such particles back to the pharyngeal portions where they are broken up.

In the line of modification represented by the subfamily Allodapinae the changes are not so great as in the foregoing since no comparable change in the structure of the pharyngeal portions is possible. The mouth opening, shown as " l ", is an interpretation based on lateral studies of this head only since I have been unable to study sufficient specimens to allow me to make an *en face* preparation but I do not think that it is in error on any important point. The most noticeable point about this head form is that the mouth opening appears to have advanced very little, functionally, from that found in " k "; most of the elaboration is restricted to the exterior of the head. There is only a slight increase in the size of the mouth opening and a slight reduction in the relative size of the pharyngeal portions. This, I suggest, is associated with the structure of the pharygeal portions which cannot by their form change in a way analagous to that in the other lines.

The same principles can be applied to the subfamily Parasubulurinae, although in this group the type of change is different because it is based on a hexagonal buccal cavity, but even here the same results as in the Subulurinae are apparent, a trend leading from a simple mouth opening in the forms " e " and " f " to complex, lobed mouth openings in " h " and " i ". The change from the relatively simple hexagonal form, " f ", to the fully triangular form, " h ", is well illustrated but no intermediate forms are available to link the

*It may be suggested that this difficulty could be overcome by increasing the size of the lumen of the oesophagus. This is theoretically possible but has not happened in practice. As I am attempting to explain the conditions as they occur, and not as they might occur, the reasoning presented above can be considered valid. From the practical aspect it may be pointed out that to increase the size of the lumen would involve a radical alteration of the entire organisation of the oesophagus, while the change in the structure of the pharyngeal portions appears to be relatively much simpler.

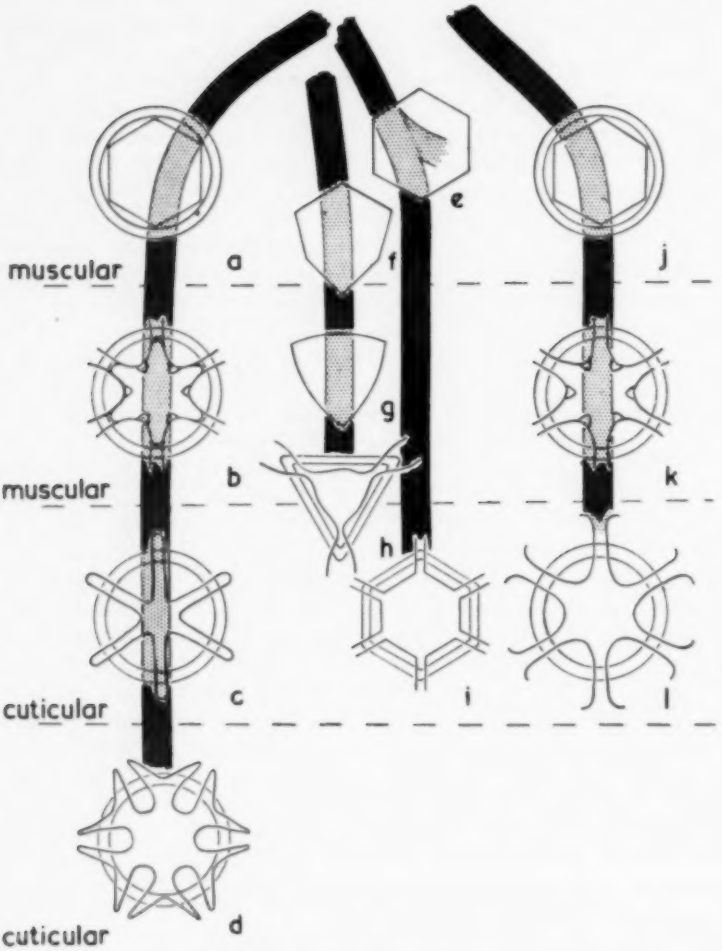


Fig. 8.—Diagram illustrating the trends in the structure of the head in the family Subuluridae Figures a, b, c, d, h, i, j, k, and l have the outline of the buccal capsule drawn. This is lacking in figures e, f, and g because it is the same as the shape of the mouth opening in all three cases. (a = *Subulura acutissima* ; b = *Subulura ortleppi* ; c = *Labiobulura peragale* ; d = *Labiobulura peramelis* ; e = *Parasubulura gerardi* ; f = *Primasubulura jacchi* ; g = *Primasubulura otolicni* ; h = *Primasubulura distans* ; i = *Tarsubulura perarmata* ; j = *Allodapa allodapa* ; k = *Allodapa baylisi* ; l = *Aulonocephalus lindquisti*.)

lobed hexagonal form, " i ", to the simple, hypothetical, hexagonal ancestral form. *Parasubulura*(*e*) may be interpreted as representing an ancestral form but may equally well be highly specialized in the structure of the pharyngeal portions. The functional reasons for the appearance of a triangular mouth opening are difficult to explain since the most immediate result must be to reduce

the flexibility of the lip-lobes, if any, although it will result, finally, in stronger structures than those based on a hexagonal form. However, for whatever reasons the tendency towards a three lipped form originated, the same tendency towards a lobed mouth opening is amply evident although the enlargement of the mouth opening has not reached the extreme shown by the " c " and " d " forms. The lip-lobes in " h " are probably, functionally, only a little more advanced than the " b " and " k " forms, although there is some reduction in the muscularity of the pharyngeal lobes associated with the " h " forms, without the lobes being free from each other. The " i " form, however corresponds fully to the " c " form in the Subulurinae, with a complement of highly developed lip-lobes which are free from each other and are attached to the remainder of the head only at their bases. Associated with this elaboration of the mouth are fully cuticular pharyngeal portions which are free from each other and can act as a triturating mechanism in a way exactly similar to that postulated for the " c " and " d " forms.

It was argued before (Inglis, 1958) that the different form of the anterior processes of the lining of the buccal cavity between the subulurin and allodapin lines on the one hand and the parasubulurin line on the other was linked to the differences in the cross sectional shapes of the buccal cavities. Thus, if the mouth openings are to function as postulated above, the lip-lobes must be able to move freely. But when the underlying processes from the buccal cavity are derived from a circular buccal cavity their ease of movement must be in inverse proportion to their width. That is, the further the processes extend round the curve of the buccal cavity the less flexible they will be and by being narrow, as they always are when associated with a circular buccal cavity, their flexibility must be improved. Such a narrowing is not required when the buccal cavity is hexagonal or triangular, as it is in the parasubulurin line ; and in this case, when lip-lobes are developed, the anterior processes from the lining of the buccal cavity are relatively wide over their full length. A similar explanation also applies to the development of the grossly lobed mouth opening of *Labiobulura peramelis*, " d ", in which there are six main lip-lobes, alternating with six smaller inter-labial-lobes. The mouth opening in this form appears to be larger, relative to the buccal cavity, than in *L. peragale*, " c", with the result that if only six lobes were present their flexibility would be impaired since they also, like the processes from the buccal cavity, hinge around a curved base. The appearance of inter-labial-lobes, whose value as gripping structures can be of only very slight importance, if any, reduces the width of the line along which the major lip-lobes bend, so improving their flexibility.

GENERAL DISCUSSION

I previously expressed the opinion (Inglis, 1958) that the lobed mouth forms had resulted from an inward extension of the edges of a hexagonal mouth opening. It is clear that this is only part of the explanation. In fact a series of correlated modifications appear to have taken place. Associated with the division or serration of the anterior edge of the lining of the buccal cavity is the appearance of a slight lobing of the mouth opening (Fig. 8 b & k), a lobing which has not greatly affected the original hexagonal form of the mouth

opening. This lobing appears to have been brought about by an increase in the tissue on the anterior end of the head to form the six " eminences " referred to above together with an increase in the length of the anterior projections of the lining of the buccal cavity. The grossly lobed mouth openings can be considered to have been derived from such a form by the further " opening up " of the mouth by the loss of the tissue between the " lip-eminences ". Thus all the diverse forms of the mouth opening can be explained as modifications of a primitively hexagonal unlobed form, all the external modification being restricted to the shape of the mouth opening itself without in any way affecting the distribution of the cephalic papillae. This interpretation is opposed to that of Chitwood & Chitwood (1950) who, in their monumental synthesis of the various forms of the head in the Nematoda, considered the subulurids to have lips " reduced to apical lobes, bearing only the internal circle of papillae . . . " and interpret *Labiobulura peramelis* (referred to by Chitwood & Chitwood as *Aulonocephalus peramelis*) as having the " rudiments of six lips (the apical lobes) separated by six interlabia." The assumption must be that they are suggesting that the lobed mouth openings found in the Subuluridae are due to the reduction of some fully six-lipped form. This is, of course, in agreement with their concept of the primitive nematode head in which the mouth is surrounded by six lips. The functional argument set out above is opposed to this and suggests that lobed mouth openings are more advanced. I further consider that the lip-lobes have been independently developed along three or four distinct lines.

OBSERVATIONS ON SOME SUBULURID SPECIES

OXYNEMA BIOCCAI Campana-Rouget, 1956

In my previous paper, in spite of referring to the paper in which Campana-Rouget (1956) described this species, I did not include it in the list of species referable to the genus *Oxynema*. This was an oversight which I wish to correct and is not to be taken as an indication that I consider *O. bioccai* a synonym of some other name.

SUBULURA INDICA Khera, 1956

Khera (1956) described this species from specimens obtained from *Loris* (*Stenops*) *lydekkerianus*. He considers it to differ from *Subulura sarasinorum* and *S. perarmata* " in possessing a divided vestibule " but he cannot have seen the redescriptions of the latter species given by Baylis (1926, 1944). It is clear that *S. indica* Khera, 1956 is indistinguishable from *Tarsubulura perarmata* (Ratzel, 1868) and, further, the discovery of more specimens of the latter species from the type host of " *Filaria* " *sarasinorum* Meyer, 1896 confirms the suggestions already put forward that *sarasinorum* is indistinguishable from *T. perarmata* (Baylis, 1944 ; Inglis, 1958).

SUBULURA VULPIS Khera, 1956.

This species was described from *Vulpes bengalensis* at Thamarwa, United Provinces. Khera does not refer to, and cannot have seen, the description of *Oxynema alata* (Mazhar, 1933) a species from *Vulpes vulpes* at Aligarh, United

Provinces. *Subulura vulpis* is clearly referable to the genus *Oxynema* and there appear to be no characters by which it can be distinguished from *O. alata*. I therefore propose that *S. vulpis* be treated as a synonym of *Oxynema alata*.

SUBULURA ARMATA Vuylstek, 1957

This species was described from *Coliuspasser macroura macroura* from the Parc National de la Garamba (Belgian Congo). Through the courtesy of Dr P. L. G. Benoit, Musée Royal du Congo Belge, I have been able to examine the types. The species is referable to the *baylisi* group of the genus *Allodapa*. This species therefore becomes *Allodapa armata*, comb. nov.

LEIPOANEMA ELLISI Johnston and Mawson, 1942

I previously referred this species, and genus, to the subfamily Parasubulurinae as a very tentative measure. It is clear that it cannot be easily fitted into the family Subuluridae at any point and, after discussion with Professor Alain G. Chabaud, I now consider it preferable to accept the subfamily Leipoaneminae Chabaud, 1957. The relationships of this subfamily to the remainder of the family are not clear but it may be diagnosed as follows :

Subuluridae : mouth opening triangular with three lip-lobes off-set from the rest of the body posteriorly by a groove ; buccal cavity triangular in cross section ; pharyngeal portions fully muscular and helically arranged. Male : precloacal sucker elongate, without definite rim or cuticular elaborations.

Type Genus : *Leipoanema* Johnston and Mawson, 1942.

REFERENCES

Baylis, H. A. (1926). Some parasitic worms from Sarawak. *Sarawak Mus. J.* **3** : 303-322.

Baylis, H. A. (1930). Some Heterakidae and Oxyuridae (Nematoda) from Queensland. *Ann. Mag. nat. Hist.* (10) **5** : 354-366.

Baylis, H. A. (1944). Notes on some parasitic nematodes. *Ann. Mag. nat. Hist.* (11) **11** : 793-804.

Berghe, Louis van den & Vuylsteke, Cl. (1938). Les Parasubuluridae, famille nouvelle d'Oxyuroides au Congo Belge. *Rev. Zool. Bot. afr.* **31** : 376-382.

Campana-Rouget, Y. (1956). Sur un nouveau subuluride de l'écureuil *Xerus rutilus* (Cretzchm, 1826). *Ann. Parasit. hum. comp.* **31** : 288-299.

Chabaud, Alain G. (1957). Sur la systématique des nématodes du sous-ordre des Ascaridina parasites des vertébrés. *Bull. Soc. zool. Fr.* **82** : 243-253.

Chitwood, B. G. & Chitwood, M. B. (1950). *An introduction to nematology*. Section I. Anatomy. Baltimore.

Inglis, William G. (1958). The comparative anatomy of the subulurid head (Nematoda) ; with a consideration of its systematic importance. *Proc. zool. Soc. Lond.* **130** : 577-604.

Johnston, T. H. & Mawson, P. M. (1940). New and known nematodes from Australian marsupials. *Proc. Linn. Soc. N.S.W.* **65** : 468-476.

Johnston, T. H. & Mawson, P. M. (1942). Some avian nematodes from Tailem Bend, South Australia. *Trans. roy. Soc. S. Aust.* **66** : 71-73.

Khera, Satendra (1956). Nematode parasites from some Indian vertebrates. *Indian J. Helminth.* **6** : 27-133.

López-Neyra, Carlos Rodriguez. (1945). Estudios revisión de la familia ' Subuluridae ' con descriptión de especies nuevas. *Rev. iber. Parasit.* **5** : 271-329.

Mazhar, A. K. (1933). On some nematode parasites of Aligarh district. *Z. Parasitenk.* **6** : 269-272.

MEYER, ADOLF (1896). Neuse ceylonische Nematoden aus Saugetieren (Filaria, Strongylus) und aus Julus (Oxyuris). *Arch. Naturgesch.* **62** : 54-82.

MOLIN, R. (1860). Trente species de nematoidi. *S. B. Akad. Wiss. Wien* **40** : 331-358.

RATZEL, F. (1868). Bechreibung eineger neuen Parasiten. *Arch. Naturgesch.* **34** : 15-156

SKRJABIN, K. I. & SCHIKHOBALOVA, N. P. (1948). [A systematic revision of the nematode family Subuluridae]. *C. R. Acad. Sci. URSS* **60** : 189-191 (in Russian).

TRAVASSOS, LAURO (1914). Contribuição para o conhecimento da fauna helmintilojica brazileira. III. Novo genero da familia Heterakidae Railliet & Henry. *Mem. Inst. Osw. Cruz* **6** : 137-318 (with English translation).

RECENT SPREAD AND PRESENT DISTRIBUTION OF THE BARNACLE *ELMINIUS MODESTUS* DARWIN IN NORTH-WEST EUROPE

BY

H. BARNES AND MARGARET BARNES

The Marine Station, Millport, Scotland

[Accepted 9th February 1960]

(With 1 figure in the text)

An account is given of the further spread of *Elminius modestus* along the German coast north of the Elbe towards the Danish coast. The population at Cuxhaven has spread to the outer estuary and *Balanus balanoides* is at several places in danger of extinction. *Elminius modestus* is now well established in several small harbours as well as on parts of the open coast between Cuxhaven and Dagbüller Hafen. The harbour populations have most probably been established by shipping but some marginal dispersion is taking place at suitable places. The species is absent north of Dagbüller Hafen : it has not yet reached Danish waters either by marginal dispersion or by a vector carrying it into any of the ports. *Elminius modestus* has not reached the north-eastern German coast.

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INTRODUCTION

Data on the present distribution of *Elminius modestus* in Europe, together with an account of the initial infection and colonization of southern England have recently been given by Crisp (1958) and Bishop & Crisp (1958). This immigrant Australasian barnacle was almost certainly carried to Holland by ships, and from the Hague district it spread rapidly northwards to reach Schiermonnikoog in 1951 (den Hartog, 1953, 1956). Although *Elminius* was established at Cuxhaven during 1953 (Kühl, 1954) there are no reports of any further northward extension of its range. North of Cuxhaven the German coast continues flat and bounded by dykes, the tide receding for great distances over mud flats ; at places there are stretches of sandy shores and off-shore sand banks. There is, however, only one major estuary, namely, that of the Eider. Further to the north in Denmark, the dykes often give way to low dunes frequently fronted with extensive mud flats. Although to the north of Cuxhaven some of the conditions, for example, high summer water temperatures over the mud flats, and long stretches of smooth coastline, are

favourable to the breeding and spread of the species, the lack of suitable surfaces for settlement over considerable distances is unfavourable to marginal dispersion. Settlement over this coastline is virtually restricted to artificial structures such as groins and harbour works. Although there are a few moderate sized harbours, usually constructed through the dykes and leading outwards to a deep channel, the smaller ' harbours ', which accommodate few ships, often consist of little more than small concrete sided channels leading to dyke gates. All these harbours usually dry out at low water. Nevertheless, during a recent survey (June-July, 1959) of German, Danish, and south Swedish coasts a considerable northerly extension of *Elminius* has been observed (Fig. 1).

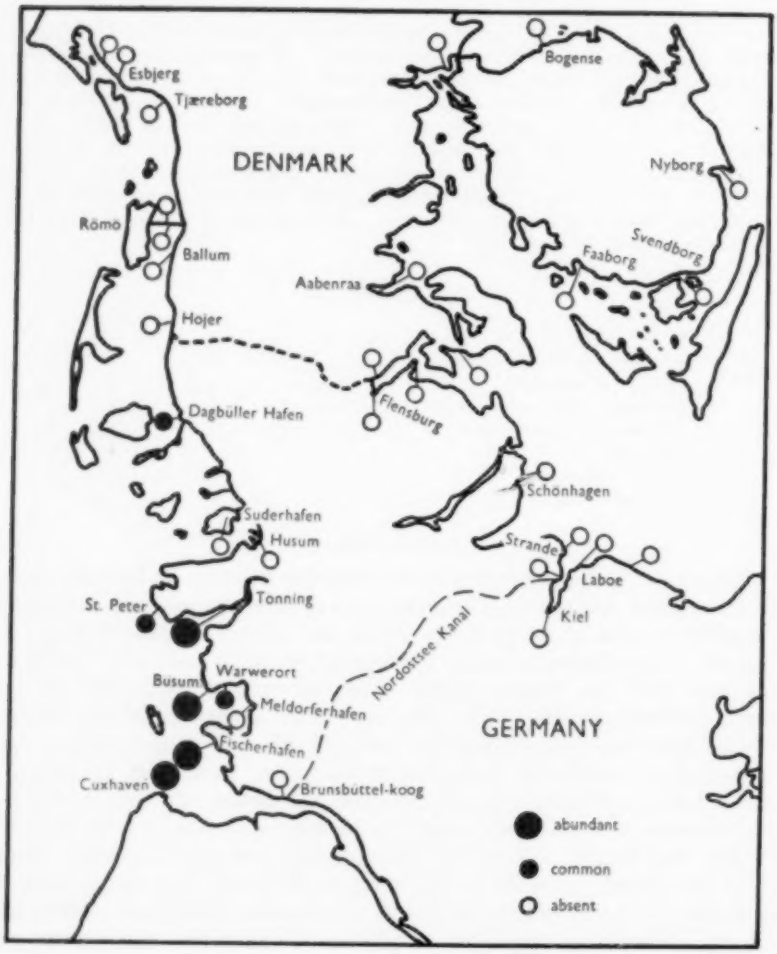

Fig. 1.—Distribution of *Elminius modestus* in north-west Europe (June-July, 1959).

GERMANY : NORTH-WEST COAST

Cuxhaven

Kühl (1953) gives no numerical estimates of the population density, but it is evident from his account that *Elminius* became well established in various parts of the harbour during 1953. In places it was present over much of the intertidal zone. At lower levels it was mixed with *Mytilus* and *Balanus improvisus* while at higher levels it was scattered amongst the *B. balanoides* ; it also extended above this second species. The outer wall of the Alte Liebe has been re-examined in detail as well as the stonework and structures at Kugelbake, which are rather more exposed than those of the Alte Liebe, being some 3 km away from the river entrance across a wide sandy bay.

B. balanoides and *B. improvisus* are still present on the Alte Liebe wall ; the latter although most frequent at the lower levels extends well into the *B. balanoides* zone—particularly under the *Fucus* covered stones and in other sheltered places. *Elminius modestus* is now not only abundant but in places (particularly at mid-to upper tidal levels) the dominant barnacle on this wall where it has to a considerable extent replaced *Balanus balanoides*. Whereas at the higher levels only large, widely spaced individuals of *B. balanoides* (11/m²), remain and then not in sufficient density to breed there are 400-600 *Elminius* /m², often aggregated and breeding freely at this level. In this upper zone spat (10-15/cm²) and young (diameter 2-3 mm) *Elminius* (3-4/cm²) are abundant. In the mid-tide zone *Balanus balanoides* is now infrequent ; all size groups of *Elminius* are present and young spat is abundant. At the lower levels, where the algal cover permits settlement, *Balanus balanoides* is still common on scattered stones and the species could still breed at this level (1-3 adults/cm²). *B. improvisus* is present at these lower levels at about the same density. *Elminius* is less frequent here, but even so in places counts gave 5-10 cyprids/cm² and young spat 17/cm². Clearly *Elminius* is rapidly replacing the indigenous species.

The rocks at Kugelbake form one side of a small harbour, the Bauhaffen, projecting seawards from the dyke. The exposure is greater, the weed cover in places less, and the accumulation of silt not so great as on the Alte Liebe wall ; the replacement of the indigenous species is clear even on casual inspection. All the available free space is densely covered by *Elminius* which, at all levels, not only occupies any spaces that become cleared of weed or *B. balanoides* but in places covers the existing population of the latter. There is even a moderate settlement of *Elminius* on the *Fucus* fronds. The mussels at the base of these rocks are covered by spat and adults as is much of the *Balanus improvisus* lower down the shore. Such *B. balanoides* as remains on the mid- and upper shores is largely found on the protected sides and under surfaces of the stones where in places groups are still present at a density adequate for breeding. This is in marked contrast to the almost continuous cover of adult *Elminius* with young spat at a density of up to 20/cm². It would seem that unless new factors intervene not for long can the indigenous species withstand the pressure of the immigrant in this area.

Brunsbüttel-koog (Sosmen-husen)

A number of small groins run seawards from the grass-fronted dykes at Sosmen-husen which is on the north bank of the Elbe some 20 km up the estuary from Cuxhaven. No barnacles were found on the mud covered rocks.

Fischerhafen

This is a small harbour set behind the dyke in Friedrichs-koog. It accommodates a small fishing fleet. *Elminius*, both adults and spat, were present on old craft that had been undisturbed for years, and on the fishing boats. It had been noticed by the fishermen. On the harbour wall small (up to 5 mm.) *Elminius* was present at 5-10/cm². It was extremely abundant on the piling at the harbour entrance—cyprids and young spat at a density of 40-50/cm²—although there were few really large individuals. *Balanus improvisus*, which was still common at the lower levels, was generally covered by a dense settlement of cyprids and spat of *Elminius*. *Balanus balanoides* was present as large scattered individuals with thick well developed reproductive organs but in most places at an inadequate density to fertilize. The impression was gained that prior to the arrival of *Elminius* the status of the indigenous species was little different.

Meldorferhafen

The harbour here is only a small channel outside the dyke. *Balanus balanoides* was present on the concrete walls and on the stones of the outer part of the dyke. They were few and consisted only of large individuals with no evidence of a current year's settlement. In a few places a breeding density was reached. *Elminius* was not found.

Warwerort

This is similar to Meldorferhafen. On a short concrete wall *Elminius* was present. Only the upper levels were seen, and here adults reached 2/dm² and spat 1/cm². It is scattered amongst the still dominant *B. balanoides*.

Büsum

This is a larger harbour set within the dyke. *B. balanoides* is still dominant at the upper and *B. improvisus* at the lower levels. The current year's settlement of the former (1-3/cm²) was showing good growth at all mid-tide levels. *Elminius* was present, both adults and spat (1-3/cm²) on the dock wall particularly at the higher levels not reached by *Balanus balanoides*. On the outer seaward side of the dock wall and the lower parts of the adjacent dyke *B. balanoides* is still dominant but *Elminius* is common with adults at a density 1/cm² and spat up to 10/cm² in places. Towards the upper levels *Balanus balanoides* is commonest in shaded localities, and here *Elminius* may be dominant, its spat in places covering the adult *Balanus balanoides*.

Tönning

This is a moderately large harbour at a break in the dyke some distance up the estuary of the Eider and situated on its north side. *B. balanoides* is

rare ; only three individuals were seen and these were covered by *Elminius* spat which formed a dense cover, most particularly on the outer seaward piles. At the harbour entrance *Elminius* was present 180 cm above the mud surface at a density of 2-4/dm² ; at 90 cm the density wss 3-4/cm², at 63 cm, 5/cm², and for a distance of some 45 cm above the mud there were 7-10/cm². Some of the individuals were clearly more than one year old but large adults were infrequent. The inner harbour, difficult of access, could not be examined.

St. Peter

This is a more exposed situation on the open coast. There is no harbour. The sandy-mud shore is backed by dunes and a long pier (about 2 km) joins the shore to a large permanent off-shore sand bank. At the base of the pier piles, 50 m from the shore, is a good growth of *Balanus balanoides* but interspersed amongst it are *Elminius* adults and at places there is some spat (1/ cm²). *Elminius* was more common (adults 54/dm² ; spat 1-5/cm²) on a nearby pipe at sand level. There were a few empty *Balanus improvisus* shells at this level.

Husum

This is a large harbour with fishing and merchant vessels and its inner parts may be considerably polluted. The inner dock walls were carefully examined from the ladders as was a side arm of the harbour. The outer part was not seen. *Elminius* was not found. *Balanus balanoides* was fairly common and the ovaries well developed even though the animals were densely covered with mud ; the density in many places was adequate for breeding.

Suderhafen

This is a small harbour on the island of Nordstrand. A short, mainly concrete, channel lies in front of the dyke and leads out to extensive mud flats. The harbour has the appearance of being little used. Large *B. balanoides* were present on the walls at breeding density and again although almost embedded in mud had well developed overies. *Elminius* was absent.

Dagbüller Hafen

This is an exposed situation. There is a comparatively long traffic pier built out from the dyke and from this a boat service runs to the offshore islands. There is no harbour. The grass dyke at the sides of the pier has a short stone wall at its base leading on to the sand. Beyond this wall are a number of large boulders. The observations were made at a high tide and it was not, therefore, possible to examine the outer face of the traffic pier at lower tidal levels. *Balanus balanoides* was common on the boulders but *Elminius* (adults 10-20/ dm²) and some scattered spat was present. The former species was still clearly dominant and the current year's spatfall had been good and was showing a good growth.

DENMARK : WEST COAST

Højer sluice

A small river traverses the dyke at this point through a short channel leading to the grass and mud flats. Barnacles were absent.

Ballum sluice

The situation is similar to that at Højer sluice and here a considerable flow of fresh water was seen to be entering the short concrete-walled channel. No marine animals were seen. It may be surmized that in both here and at Højer the entry of fresh water was sufficiently great to prevent the development of a truly marine fauna. Only a small quantity of sea water will be brought into these channels for short periods at high tide.

Rømø dyke

This is a causeway connecting the mainland to Rømø, and leading across the very extensive marshes. It is of particular interest because it lies directly across the path of any inshore south-north drift. The side of the causeway is mainly grass, but where it abuts on the mud is a low stone wall which is reached by the tide. *Balanus balanoides* was present but infrequent, with adults at 10/dm² and spat 18/dm² on the north side ; much of the current year's settlement had grown slowly to reach a size of only 3 mm by July. *B. balanoides* was even less common on the south side. *Elminius* was absent.

Tjæreborg

To the south of the village there are extensive mud flats backed by low dunes not carrying a dyke. From the dunes groins, in the form of hollow concrete blocks, extend some 20 metres seawards at intervals. Beyond this the tide recedes for 1-2 km. These ' blocks ' retain water as the tide recedes and *Balanus balanoides* and *B. improvisus* were present on their inner sides, the former being commoner at the upper levels. *Elminius* was absent.

Esbjerg

In view of the considerable amount of shipping—both fishery and mercantile—this is an obvious point of entry for the immigrant into Danish waters. The harbours were carefully searched on three separate occasions including the following locations : the outer wall of the main Traffic Harbour facing the sea ; the inside of this harbour including the inner sea wall, lateral walls and any structure in the harbour ; head of the Fish Harbour and its right wall ; wall of new harbour under construction ; England Quay jetties and those to the south. *Balanus balanoides* was abundant on all suitable substrata, often covered by mud in the inner harbours. The current year's spat showed good growth. At the lower tidal levels *B. improvisus* was common. *Elminius* was absent.

DENMARK : OTHER COASTAL AREAS

A detailed survey has been made of the barnacles round the shores of all the islands, visits being made to most of the ports and fishing villages. Particular attention was paid to places where *Elminius* might have been expected. It was absent over the whole coast.

GERMANY : NORTH-EAST COAST

In view of the possible entry of *Elminius* to the Baltic via the Kiel canal from the well established population at the mouth of the Elbe in Cuxhaven, a careful search was made of the eastern environs of the canal. The stones, boulders, and pier structures at Strande, Holtenau, Kiel harbour, and Laboe on the Kieler Forde were thoroughly examined. *Elminius* was everywhere absent.

DISCUSSION

The salient points that emerge from these observations are : first, *Elminius modestus* has consolidated its position in the Cuxhaven area, where *Balanus balanoides* is in danger of extinction. Secondly, north of Cuxhaven almost to the Danish border *Elminius modestus* is now present and in places abundant and even dominant. Thirdly, *Elminius modestus* has not reached the Danish, Swedish or north-eastern German coasts. Both marginal and remote dispersal are involved in the spread.

The population at Cuxhaven was considered by Crisp (1958) to be a coastwise extension of that which reached Schiermonnikoog in 1951 and whose spread was rapidly accelerated along the Friesian archipelago. The evidence presented by Kühl (1954) suggests very strongly, however, that the Cuxhaven population was not established by marginal dispersal : he points out that in the autumn of 1952 *Elminius*, although present, was not common on the east Friesian coast and yet by late 1953 it was well established in the Cuxhaven harbours. During the summer of 1953 a large number of craft were on three occasions concentrated in the harbour because of storms and he considers the population was established during these periods. The more recent spread has extended at least to the limits of the estuary at Kugelbake and the replacement of *B. balanoides* has proceeded rapidly. The present situation is very similar to that already described by Crisp (1958) for places where *Elminius* has almost displaced *B. balanoides* in Britian ; large isolated *B. balanoides* remain amongst the dense *Elminius* cover. The present observations suggest that this replacement begins by *Elminius* first occupying any available areas and the higher tidal levels. Space is thus denied to the annual *Balanus* spatfall. In places where the indigenous barnacle cover has been extremely dense the formation of hummocks which eventually break away materially helps this process (Barnes & Powell, 1950). Furthermore, any grazing by *Patella* which may remove the young *Balanus balanoides* spat helps to clear areas which are occupied later by the repeated spatfalls of *Elminius* during the summer. It is in this way that typical large conical and securely attached adult *Balanus balanoides* become isolated in the *Elminius* cover. With increasingly heavy *Elminius* spatfall, smothering of the indigenous species takes place ; settlement does, of course, take place on adults with a heavy spatfall even in the early stages of colonization. It is worth noting that *Elminius* is far less self-destructive than *Balanus balanoides* for, although when dense the characteristic star-like shape is lost, growth rarely seems to lead to the exaggerated columnar forms only lightly attached to the substratum, as is the case with *B. balanoides*.

The advantages of *Elminius* over *Balanus balanoides* in their mutual competition have been listed and commented upon by Crisp (1958). One further

asset may be noted ; the fact that *Elminius* will settle and survive at higher tidal levels than *Balanus balanoides* means that in the initial stages of colonization a population can be established at this level *without* competition with the indigenous species. When this high level population reaches breeding density there is a local supply of larvae often through several months that is available for encroachment on the *B. balanoides*.

Both remote and marginal dispersal appear to be concerned in the spread that has just been described. The colonization of the outer estuary of the Elbe at such places as Kugelbake is clearly marginal dispersion from the Cuxhaven population. The distance between Cuxhaven and Dagbüller Hafen is some 150 km and at a rate of spread of 30 km/year (Crisp, 1958) all the places along this coast could have been colonized by marginal dispersal. This does not, however, seem to have been the case. First, there are long stretches of coast where settling surfaces are virtually absent and where, therefore, a reduced rate of spread would be expected. Secondly, there is no well-marked advancing front ; the isolated populations, largely restricted to harbours, are of similar status to one another and as far as can now be ascertained have been established for several years. It may be confidently surmised that the isolated populations at Fischerhafen, Büsum and Tönning have been intiated by fishing boats acting as vectors. Colonization has then been similar to that of the separate estuaries of south-west England or the independent more widely spaced centres of the French coast (Crisp, 1958 ; Bishop & Crisp, 1958). It should be pointed out that this type of dispersal need not involve traffic between the ports or harbours concerned ; it only requires boats to fish in the water containing abundant larvae. Where a colony has been established in these small muddy harbours it has rapidly expanded to become the dominant barnacle. Often it would appear that competition has been relatively restricted ; the indigenous *B. balanoides* population at Meldorferhafen and Suderhafen for example would offer little resistance to the colonization by *Elminius* and such was probably the case at Tönning. It would seem that the indigenous population in such places is gradually built up over a number of years from small annual spatfalls ; in the absence of competition from algae and freedom from the normal predators the animals may live for many years even in the presence of much mud.

The absence of *Elminius* from Meldorferhafen and Suderhafen is almost certainly due to the isolation and absence of fishing boats. It was surprising not to find it at Husum ; parts of the inner harbour were carefully examined but the outer structures appeared difficult of access and were not seen.

At two places, St. Peter and Dagbüller Hafen, the infection seems most likely to have been by marginal dispersion without the intervention of any vector ; both places are on the open coast and do not have harbours. St. Peter is only some 20 km from the dense population at Tönning which could well be the source of this settlement. Dagbüller Hafen is, however, 50 km to the north and may have been infected from a population at Husum that was not found, or from the islands which were not investigated.

Northwards from Dagbüller Hafen into Denmark the coast is not suitable for settlement—there are few substrata over wide stretches of the coast before Esbjerg is reached (a distance of 80 km), where the advancing front of a

marginal dispersal could be established. Any northward inshore spread would almost certainly have been detected on the Rømø causeway. The absence at Esbjerg—in view of the considerable amount of shipping entering the various harbours, much of it from places where *Elminius* is well established—is at first sight surprising. However, much traffic ties up at open quays and the main Traffic Harbour, except for a small channel, empties between tides. Containment of any immigrant larval population is minimal under these conditions. Possibly a harbour such as that at Copenhagen is more likely as the initial point where *Elminius* could be introduced into Danish waters.

ACKNOWLEDGMENTS

We wish to acknowledge a grant from the Browne Fund of the Royal Society for a programme of work of which that reported above is a part, and to thank Miss Ann Lawson for her assistance.

REFERENCES

Barnes, H. & Powell, H. T. (1950). The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides* after a heavy initial settlement. *J. anim. Ecol.* **19** : 175-197.

Bishop, M. W. H. & Crisp, D. J. (1958). The distribution of the barnacle *Elminius modestus* Darwin in France. *Proc. zool. Soc. Lond.* **131** : 109-119

Crisp, D. J. (1958). The spread of *Elminius modestus* Darwin in north-west Europe. *J. mar. biol. Assoc. U.K.* **37** : 483-520.

den Hartog, C. (1953). Immigration, dissemination and ecology of *Elminius modestus* Darwin in the North Sea, especially along the Dutch coast. *Beaufortia* **4** : 9-20.

den Hartog, C. (1956). Speculations on the immigration of the barnacle *Elminius modestus* in France. *Beaufortia* **5** : 141-142.

Kühl, H. (1954). Uber des Auftreten von *Elminius modestus* Darwin in der Elbmundung. *Helgoländer Wiss. Meeresuntersuch.* **5** : 53-56.

DIET, LONGEVITY AND DENTAL DISEASE IN THE SIERRA LEONE CHIMPANZEE

BY

T. S. JONES, O.B.E., M.Sc., C.M.Z.S.
Agriculture Department, Njala, Sierra Leone

AND

A. J. E. CAVE, M.D., D.Sc., F.Z.S.
University of London

[Accepted 9th February, 1960]

(With 4 plates)

The Sierra Leone chimpanzee has adapted its dietary and feeding habits to the changed ecology resulting from replacement of high forest by secondary forest and from the extensive development of agriculture in the latter. Much of the animal's food is now procured, easily and in abundance, from native farms and gardens ; it differs qualitatively from the traditional high forest diet. One consequence of this new, constant and abundant food supply appears to be an increased longevity. Another is the high incidence of dental mischief from the mastication of infected food material obtained from the refuse heaps around native habitations.

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INTRODUCTION

It seems very probable that, in Sierra Leone during recent years, the life-span of certain originally high forest-dwelling mammals (including the chimpanzee and various monkey species), which are omnivorous feeders and capable of ready adaptation to ecological changes, may have been extended. In the course of the past century the human population of Sierra Leone has increased enormously and agriculture has consequently expanded so as now to constitute the principal economic activity. The great spread of upland farming (by the traditional ' bush fallow ' or ' shifting cultivation ' method) has involved the destruction of large areas of the original high forest and its replacement by low, dense secondary forest (' farm bush '). Moreover, numerous areas under this latter type of vegetation are also rotationally cut and burnt every few years to make farms, so that most of the land formerly under high forest is now either under secondary forest or else constitutes farm land. Indeed high forest now remains only as forest reserves, as narrow strips bordering rivers and as isolated patches in hillside gullies, as ' sacred bush,' etc.*

* For a map illustrating the diminished remnant of high forest in relation to farm bush, consult Roy Lewis, *Sierra Leone*, p. 77. (London : H. M. Stationery Office, 1954).

As a consequence the chimpanzee, having become adapted to a (mainly) secondary forest habitat and therefore to a wider food range, now can, and does, subsist very largely upon a variety of farm crops, thus utilising an abundant and readily procurable supply of soft and easily digested food. This is repeatedly evidenced by the frequency with which chimpanzees are seen on and about farms and by the continual reports of the unmistakable damage they inflict upon the crops.

The availability of a wider range, and more plentiful supply, of softer (i.e. more easily masticated) food most probably tends towards an extension of the average chimpanzee life-span. This notion receives support from the not infrequent examples encountered of wild-shot, very old chimpanzees which manifest a dental deterioration incompatible with subsistence upon the relatively scanty and more fibrous food material available in the high forest. Such specimens reveal all the anatomical signs of extreme age, together with a loss, wear or disease of the dentition so severe as to suggest most forcibly that survival was wholly dependent upon the availability of abundant, cultivated and easily masticated food material.

Field observations in Sierra Leone have shown that chimpanzee diet in the high forest includes the bases of the young, unopened leaves and the mesocarp of the fruit of the oil palm (*Elaeis guineensis*), bamboo shoots, wild yams, fruits, leaves, grubs found in forest debris, snails and (probably) young birds and eggs. Doubtless the wild chimpanzee is much more carnivorous than is commonly supposed and Stanley (1919) comments that ' practically every native hunter in Sierra Leone states most definitely that chimpanzees catch and devour fish with skill and avidity ' and proceeds to describe some of the chimpanzee methods of catching. In secondary forest, with its farms, the diet embraces (apart from various wild fruits and leaves) cultivated yams, bananas, plantains, pineapples, sweet potatoes, sweet cassava, maize, mangoes, pawpaws, okra, groundnuts, and the leaves of various cultivated plants.

The abundance and accessibility at all seasons of this ' softer ', nutritious and well-localised food material, requiring minimal masticatory effort, considerably lightens the chimpanzee's burden of food gathering. Being thus assured of a constant, plentiful and easily obtained food supply and having no (or extremely few) natural enemies, the chimpanzee inhabiting secondary forest might therefore reasonably be expected to enjoy a greater longevity than was formerly possible under the conditions of life obtaining in the anciently widespread high forest. It is of course impossible to establish by any scientific standard the relative longevity of chimpanzees from these two dissimilar habitats but it is equally impossible to ignore the observational evidence to hand as to the increasing numbers of mature and very old chimpanzees encountered in cultivated areas, or killed by the native hunters. And it is hard to believe that the extremely old and practically edentulous animal, whose skull is noticed in detail below, could possibly have survived to such obviously advanced age under conditions other than those obtaining in a secondary forest habitat.

DENTAL DISEASE IN THE WILD CHIMPANZEE

The easier living conditions presented to the wild chimpanzee in Sierra Leone by the continuous expansion of agriculture would seem to exact, in return for an increased life-span, a certain toll in the form of dental (or parodontal) disease.

Excluding congenital conditions (e.g. numerical, positional and morphological variations of the teeth) and the effects of trauma, the pathology of the chimpanzee dentition is conveniently classified under four heads, viz. hypoplasia, caries, dental abscess and parodontal disease. The relative incidence of these several conditions in a small series (ten) of wild-killed Sierra Leone chimpanzees is not without significance. This series includes nine adult animals: of these, three manifest hypoplasia of the teeth (two mildly, one very severely) and seven display some degree of parodontal disease (three incipiently, four emphatically). One of the four skulls exhibiting pronounced parodontal disease—that of an extremely old animal—is so strikingly pathological as to warrant description and consideration herein : for the severity of the pathological change present, and the degree of physical disability occasioned thereby during life, constitute, if not absolute proof, then at least the strongest possible suggestive evidence that this particular animal had attained its obvious great age solely because of the easier feeding conditions afforded it in a secondary forest habitat.

Hypoplasia

This curious condition of pitting and of transverse and longitudinal striation of the dental enamel is of undetermined genesis. Both a febrile illness during early life and a primary defective constitution of the enamel have been invoked as causative. In *Homo* the condition may be hereditary. Colyer (1936) gives its incidence for anthropoid apes as *Gorilla* 8 per cent, *Pan* 11 per cent, *Pongo* 17 per cent and *Hylobates* 4 per cent. It is frequent also in *Papio*, *Cercocebus* and *Colobus*, and is known in *Cebus* and other Platyrrhini. The three Sierra Leone chimpanzee skulls exhibiting dental hypoplasia come from the same locality, viz. Makpele chiefdom, Pujehun District, near Zimmi. Details are as follows :

Specimen 1 (Ref. C 2.24) ad. ? sex.

The maxillary incisors show faint transverse grooving.

Specimen 2 (Ref. C 2.25) ad. ♂.

The maxillary and mandibular incisors and the maxillary canines and premolars show faint transverse grooving. A deeper, more emphatic, groove demarcates the tip of the mandibular right canine.

Specimen 3 (Ref. C 2.22) ad. (not aged) ♀.

Occipito-mastoid and inter-premaxillary sutures open : basioccipito-sphenoidal synchondrosis present : third molars unworn : a full dental complement present at death : some teeth lost thereafter.

A severe degree of hypoplasia affects the incisors, canines and pre-molars of both upper and lower jaws. The maxillary central incisors are so deeply and continuously grooved transversely as to be almost subdivided. The tips

of the right maxillary and of both the mandibular canines are severally demarcated from their respective tooth bodies by a deep horizontal groove : the upper and lower premolar teeth are likewise ' peg-topped ' from grooving. The thus partly isolated tip of the left maxillary canine has anciently broken off through the plane of grooving and a false occlusal surface has been consequently developed. Additionally to these major grooves, minor transverse striae are present on the incisors and canines. The severity of the grooving is depicted in Pl. 1.

Caries

Caries occurs in two distinct forms—caries of the enamel and caries of the dentine. The former condition is extremely rare in all wild animals. Colyer (1936) gives its incidence for the wild chimpanzee as 4·5 per cent. His examination of 289 skulls of *Cercopithecus mona grayi* from the Batouri District of the Cameroons revealed thirty-one examples of dental caries, only one of which represented caries of the enamel (0·34 per cent incidence). Caries of the dentine (and cementum) is usually the sequel to tooth-injury. None of the nine Sierra Leone chimpanzee skulls exhibits enamel caries. Caries of the dentine occurs in one skull (Ref. C 2.30), that of a very old female with marked parodontal disease (and noted below). Herein the cervical aspects of the mandibular right 1st and 2nd molars display each a well established caries cavity. Abscess formation has not resulted.

Dental abscess

This may result from injury to the dental tissues or may supervene upon a carious dental condition. The lesion was absent from all the Sierra Leone specimens.

Parodontal disease

This lesion begins as a marginal gingivitis, which spreads to and involves the alveolar bone and the periodontal membrane, resulting in progressive loss of the periodontal tissues and a consequent loosening and even shedding of the teeth. The initial injury to the gum is commonly effected by adventitious hard particles in the food. The formation of ' pockets ' between contiguous teeth and the extension of these into the alveolar bone is a prominent feature of the disease, as is also the exposure of the roots of the teeth. Colyer (1936) holds that ' the disease is caused by an alteration in the character of the diet . . . either of a physical or of a chemical nature—in other words by a departure from natural diet and conditions.'

Parodontal disease is present in no less than seven of the nine adult Sierra Leone chimpanzee skulls, incipiently in three, well established in three others and excessively severe in one. This is a remarkably high (77 per cent) and significant incidence. The affected specimens may be briefly detailed as follows:

Specimens manifesting incipient parodontal disease

Specimen 1 (Ref. C 2.24) ad. ?sex.

Makpele chiefdom, Pujehun District, near Zimmi.

The palatal root of the upper left 2nd molar is exposed from alveolar absorption.

Specimen 2 (Ref. C 2.22) ad. (not aged) ♀.

Makpele chiefdom, Pujehun District, near Zimmi.

There is alveolar regression on the buccal aspect of the lower left 1st molar.

Specimen 3 (Ref. C 2.19) ad. (aged) ♂.

Barri chiefdom, near Potoru.

Around all the maxillary teeth there is a slight but distinct degree of alveolar absorption.

Specimens manifesting established parodontal disease

Specimen 1 (Ref. C 2.26) ad. ♂.

Barri chiefdom, near Potoru.

A moderate and generalized degree of alveolar absorption affects all the upper and lower post-canine teeth. The palatal aspects of the roots of both upper 1st molars are exposed. There is extensive loss of alveolar bone on the lingual and buccal aspects of the lower right 2nd premolar and first two molars, and a corresponding loss around the lower left 2nd premolar. The now missing lower right 1st molar had undergone extensive exposure of its anterior root and was evidently loose in life.

Specimen 2(Ref. C. 2.31) ad. ?sex.

Perri-Gallinas chiefdom, near Bumbe.

Both the upper and lower jaws show a generalized alveolar rarefaction and absorption. The buccal roots of the upper right 1st molar are exposed. A food ' pocket ' is present between the upper left 1st and 2nd molars.

Specimen 3 (Ref. C 2.30) ad. ♀.

Makpele chiefdom, Pujehun District, near Zimmi.

The skull of an extremely old animal : crown wear is extreme and no trace remains of facial or cranial sutures.

Alveolar absorption is everywhere pronounced. The anterior buccal root of the lower left 1st molar is exposed. All the upper incisors, the upper left canine and the lower right canine have been lost during life but probably not solely as the result of the parodontal mischief present. The alveolar margin in the region of these lost teeth has undergone considerable recession : it has that curious ' spongy ' appearance characteristic of parodontal change and it retains indications of the sockets of the absent teeth in the form of shallow indentations. The healing after tooth-loss has been the healing of chronically inflamed bony tissue. Yet the retention of the lower incisors and of all the post-canine teeth, despite individual tooth-looseness and a generalized alveolar absorption, suggests that the anterior teeth were lost from injury. A food ' pocket ' is present between lower right 1st and 2nd molars and, as noted, each of these teeth has developed a cervical caries of the dentine. For a long time before death, the only occlusion possible was that between the upper and lower molars, the upper right canine being unopposed inferiorly and the lower incisors, left canine and 1st premolar being unopposed superiorly. Much of the ' bite ' was therefore by means of the upper gum while the loss of an upper canine and its contralateral lower fellow must have proved a severe physical handicap both in biting and in mastication. The dental disabilities present

suggest most forcibly that this particular animal could not have attained its very obvious extreme old age had it not had ready access to a constant supply of easily procurable and readily digestible food material.

Specimen 4 (Ref. C 2.27) very old ♀.

Barri chiefdom, near Potoru.

Orbital, facial and cranial sutures long obliterated : occlusal surfaces of upper 2nd molars enamel-denuded : surviving teeth crown-worn almost to their necks : only 13/32 teeth *in situ* at death.

Of the upper teeth, the incisors, right 1st premolar and 1st molar have been shed long before death : their alveoli are filled with bone of that ' pumice stone ' appearance characteristic of chronic inflammation. At death the right canine and the left 1st premolar lay loosely (almost unattached) within shallow, diseased sockets, whence they have since escaped : the left 3rd molar (since lost) was attached by but the apex of a single root. The surviving left 2nd premolar is retained *in situ* by its palatal root only, its two buccal roots being almost entirely exposed by absorption of their alveolar walls. The surviving left canine is worn down almost to gum level.

Chronic bone infection of the right premaxillary region has produced a marked asymmetry of the infranarial portion of the skull and the infective process therein was obviously active at the time of death.

Of the lower teeth, the left canine and 1st premolar and the right 3rd molar alone remained at death : the left 3rd molar may have maintained a precarious attachment by the apices of its roots or may recently have been shed. The right 2nd molar was certainly shed from a resorbed diseased socket not very long before death for the socket remains unhealed. The left canine is a mere stump from abnormal and excessive crown attrition.

The alveolar margin everywhere shows the typical ' pumice stone ' appearance of severe parodontal disease.

The glenoid fossae for the mandibular condyles are flattened and distorted from obliteration of their articular eminences.

Owing to the faulty ' bite ' mastication must have been effected under the most adverse mechanical conditions. Some right-sided occlusion was possible between the (surviving) upper and lower molars, but the isolated loose 2nd premolar bit only against the lower gum : the length of the (now lost) upper canine is unknown. If this tooth were longer than its contralateral fellow it bit against the mandibular gum ; but if of equal length it fell short thereof. The right upper and lower 3rd molars had not been in occlusion for a very long period before their ante mortem shedding. The three surviving left maxillary cheek teeth occluded with the mandibular gum only.

The stump of the left upper canine probably engaged with the ipsilateral mandibular 1st premolar, but it has also been brought into an abnormal occlusion with the much abraded left mandibular canine. So abnormal a ' bite ' must have involved some backward displacement of the mandibular condyle and a stretching of the capsules of the temporo-mandibular joints. The physical disabilities resulting from the loss of so many of the teeth from advanced

parodontal disease is perhaps best appreciated from the accompanying photographs of the specimen (Pls. 2, 3).

It is obvious that so dentally handicapped an animal could not have sustained life on a strictly ' natural ' diet and that its survival to so great an age was due to the compensatory food facilities provided by native gardens and farmlands.

DISCUSSION

The Sierra Leone chimpanzee has adapted itself, almost of necessity, to the changed ecological conditions brought about by the extensive destruction of its former high forest habitat and the notable development of agriculture in the resultant secondary forest. Field observations and the spoils of native hunting strongly suggest that this animal, in consequence of its changed feeding habits, now attains a greater longevity than that formerly possible under the more stringent living conditions of the high forest.

It would appear that these longer lived animals display a relatively high incidence of parodontal disease. This may be attributed not only to the altered dietary already noted but also to the habit developed by chimpanzees of exploring the refuse heaps which abound in the neighbourhood of native farms and settlements. For these refuse heaps, composed of decaying animal and vegetable matter, contain not only material likely to prove mechanically injurious to the gingival and interdental mucosa but also much highly infective material.

This chimpanzee habit of refuse heap exploration for food material has been noted by Merfield (1936) in the Batouri District of the Cameroons, and Colyer (1936) has reported and figured two examples of well established parodontal disease in animals from that region, though in neither is the disease so advanced as in the Sierra Leone specimen C 2.27.

It is instructive to compare the dental pathology manifested by the wild-shot specimen C 2.27 herein with that obtaining in a long-captive animal, viz. the male chimpanzee, ' Jimmie ', which lived in the mengerie of the Zoological Society of London from 1923 to 1946 and was therefore at least 24 years old at death. The teeth of this animal exhibit a marked generalized hypoplasia, most pronounced on the non-molar teeth in both the upper and lower jaws. Parodontal disease is present and affects practically every tooth. There is marked recession of alveolar bone with consequent root exposure, most emphatic on the lingual aspect of the upper cheek teeth, which display deep and old-standing ' food pockets ' between each contiguous pair. In the right maxilla the sockets of both the 2nd premolar and the 2nd molar have been the site of peridental abscesses effecting great destruction of alveolar bone. The premolar abscess has burst externally into the cheek, the molar abscess internally into the palate : the two teeth concerned remain attached by their root tips only. A ' food pocket ' is present behind the lower right 2nd molar which is loose in its socket. Caries is absent, no tooth has been lost during life and the mechanics of the ' bite ' have remained undisturbed (Pl. 4).

This long-captive animal obviously subsisted on a diet different from that obtainable under natural high forest conditions and one more akin to the diet

of the wild Sierra Leone chimpanzee living in cultivated secondary forest. In both C 2.27 and the captive animal parodontal disease has ensued, doubtless as the result of alterations in the physical or chemical nature of the diet. But in the captive specimen there is very much less destructive change of a chronically infective nature : the alveolar margins have indeed undergone absorption but they manifest no development of the ' pumice stone ' appearance so characteristic of C 2.27. The inference is that the healthier state of the dentition of the captive animal is the consequence of its being provided with clean, non-infected food during its confinement and that the advanced pathological state of the dentition in the wild animal results largely from the eating of infected food material.

ADDENDUM

Since the above was written the skulls of three additional wild-shot Sierra Leone chimpanzees have become available for examination. All three animals had retained at death a complete and healthy dentition and all manifest some degree of hypoplasia of the anterior maxillary and mandibular teeth. None shows any evidence of caries or of dental abscess. In one skull, that of an old female, a solitary food ' pocket ' has been present and thereabout is evidence of incipient parodontal disease.

Details of the three specimens are as follows :

Specimen 1 (Ref. C 2.32) ad. ?sex.

Gaura chiefdom, Kenema District.

Dentition complete, normal and healthy, with alveolar and interalveolar bone everywhere well formed. The incisors, canines and premolars of both the upper and lower jaws exhibit a mild degree of hypoplasia.

Specimen 2 (Ref. C 2.33) ad. (very old) ♀.

Gaura chiefdom, Kenema District.

Dentition complete and severely crown-worn. Alveolar bone everywhere healthy and well formed.

No food ' pockets ', dental decay or parodontal mischief present. The canines and first premolars of both the upper and lower jaws display a very slight degree of hypoplasia.

Specimen 3 (Ref 2.34) ad. (oldish) ♀.

Gola Forest, near Liberian border.

Dentition complete at death. Teeth well formed and healthy and alveolar bone generally well formed.

There is mild hypoplasia of the maxillary incisors, canines and first premolars and of the mandibular incisors, canines, first and second premolars. A food ' pocket ' has been present between the mandibular right second premolar and first molar, in which region there is some resorption of the buccal and lingual alveolar margins and of the interalveolar septum between the two teeth concerned, whose roots are consequently unduly exposed. These changes represent an initial stage in the development of parodontal disease.

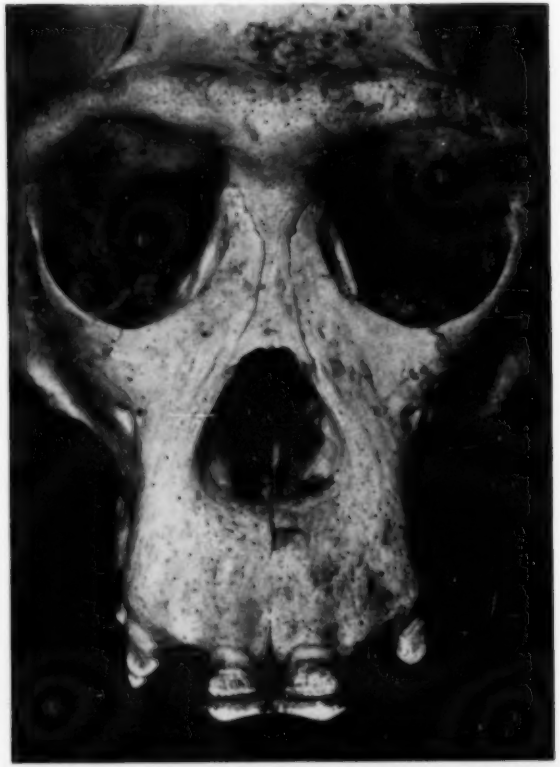

Fig. 1.—Chimpanzee (C 2.22) ad. ♀. Cranium, frontal aspect. Dental hypoplasia. The upper medial incisors and right canine are deeply grooved horizontally. The tip of the left canine has become detached through the line of grooving.

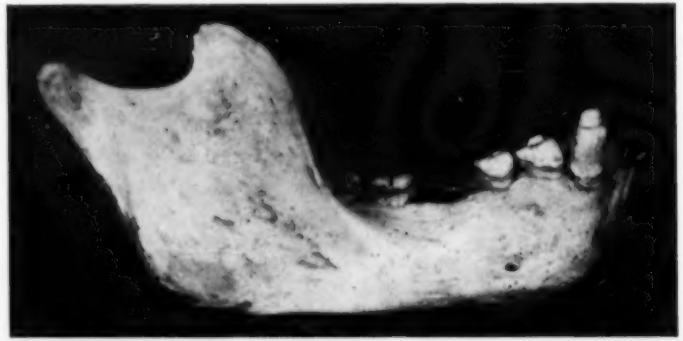

Fig. 2.—Chimpanzee (C 2.22) ad. ♀. Mandible, dextral aspect. Dental hypoplasia. The tips of the canine and premolars are sharply circumscribed by deep horizontal grooves.

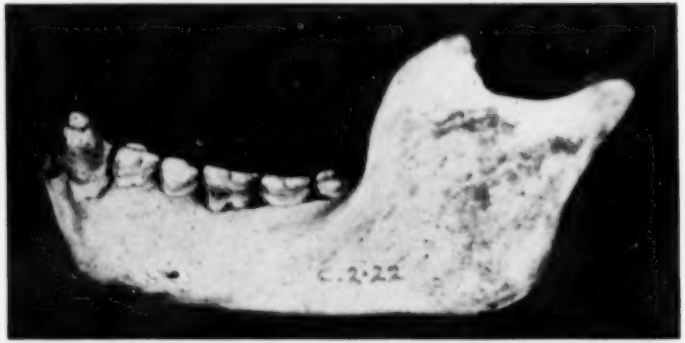

Fig. 3.—Chimpanzee (C 2.22) ad. ♀. Mandible, sinistral aspect. Dental hypoplasia. The tips of the canine and 1st premolar are sharply circumscribed by horizontal grooves.

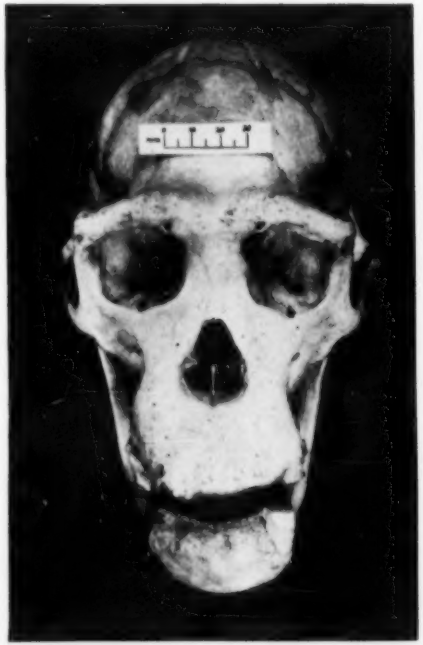

Fig. 1.—Chimpanzee (C 2.27) aged ♀. Parodontal disease. Skull, showing loss of anterior teeth and the worn-down condition of the surviving canines.

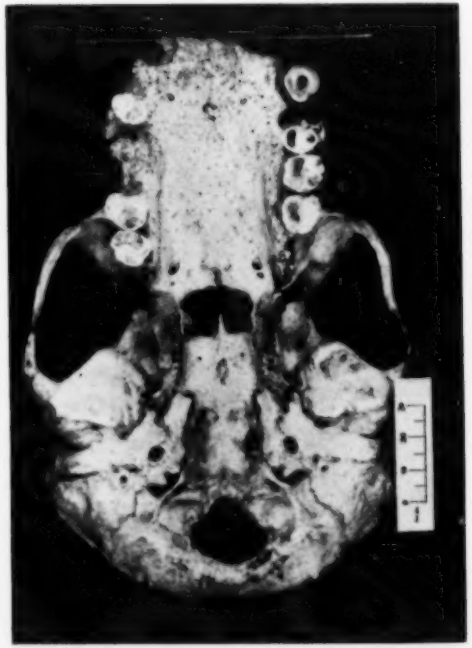

Fig. 2.—Chimpanzee (C 2.27) aged ♀. Parodontal disease. Palate and maxillary dentition, to show tooth-loss, attrition of left canine and the severe crown-wear of the surviving teeth.

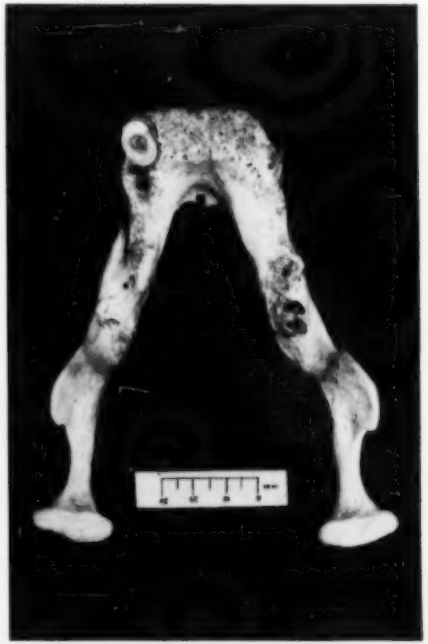

Fig. 3.—Chimpanzee (C 2.27) aged ♀. Parodontal disease. Mandible, to show excessive tooth-loss, chronically inflamed alveolar bone and attrition of the surviving canine.

Fig. 1.—Chimpanzee (C 2.27) aged ♀. Parodontal disease. Skull, dextral aspect. To show excessive tooth-loss and non-occlusion of the surviving teeth. (The mandible is somewhat advanced in articulation).

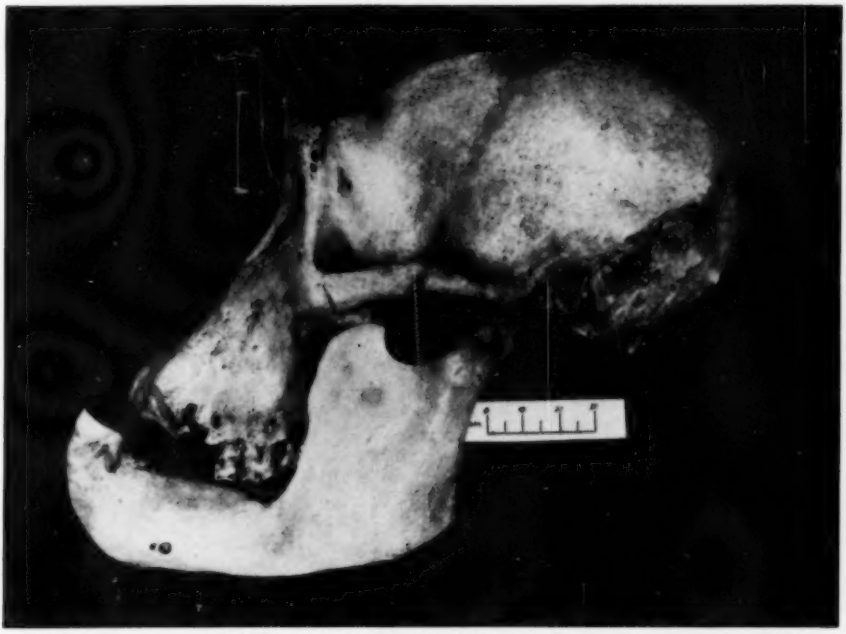

Fig. 2.—Chimpanzee (C 2.27) aged ♀. Parodontal disease. Skull, sinistral aspect. To show tooth-loss, condition of alveolar margins, non-occlusion of maxillary teeth and the extreme reduction of the canines. (The mandible is somewhat advanced in articulation.)

Fig. 1.—Chimpanzee ("Jimmie") ♂. 24 years in captivity. Parodontal disease. Dextral aspect of the complete dentition. To show generalised recession of alveolar bone, exposure of an upper 2nd molar root and abscess-sinus above upper 2nd premolar.

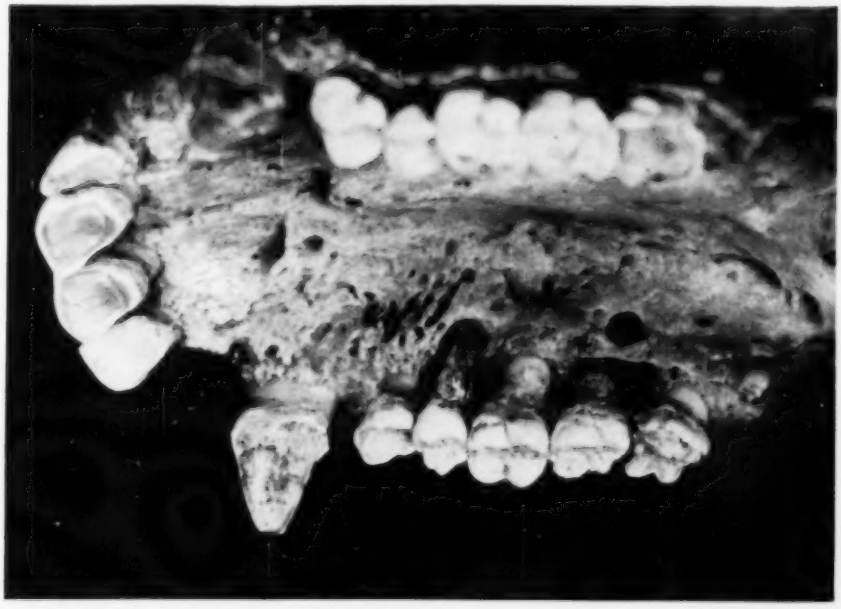

Fig 2.—Chimpanzee ("Jimmie") ♂. 24 years in captivity. Parodontal disease. Oblique inferior aspect of right maxillary teeth. To show generalised recession of alveolar bone, the presence of interdental food pockets, and extreme root exposure with abscess formation in connexion with the 2nd premolar and 2nd molar. The palatal orifice of the molar abscess-sinus is apparent.

REFERENCES

COLYER, J. F. (1936). *Variations and diseases of the teeth of animals.* London : Bale, Sons & Danielsson.

MERFIELD, F. G. (1936). Quoted by Colyer (*op. cit.*, p. 674).

STANLEY, W. B. (1919). Carnivorous apes in Sierra Leone. *Sierra Leone Studies* **1919** : 3-19.

NOTICE

[" Proceedings', Vol. 134, Part 4, was published on 2nd September 1960]

Printed by Taylor & Francis, Ltd., Red Lion Court, Fleet Street, London, E.C. 4

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